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An Introduction to
VERTEBRATE ANATOMY

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An Introduction to
VERTEBRATE ANATOMY

HAROLD MADISON MESSER, *Long Island University*

REVISED EDITION

THE MACMILLAN COMPANY NEW YORK 1947

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To the Memory
of
My Father
who ever cherished the hope
that I become
A Teacher of Youth

Preface to Revised Edition

In the preparation of this Revised Edition of *An Introduction to Vertebrate Anatomy* the author has had in mind three main objectives: first, to make the book somewhat more complete for a one-semester course; second, to improve the quality, and increase the number, of the illustrations; and third to correct or qualify certain statements that recent investigation has shown to be questionable.

Several teachers who have used the original book in the classroom have suggested the expansion of certain subjects which they felt were not adequately treated. Others have found the book to be somewhat short and incomplete, even for a one-semester course. The author, agreeing in general with these comments and suggestions, has gone over the text carefully, and has not only expanded many portions of it, but has also added considerable new material. As a result, the Revised Edition is about ten per cent larger than the original.

In the matter of illustrations a number of changes have been made. Many of the figures have been enlarged, a number have been entirely redrawn and relabeled, and over twenty new ones have been added.

Although the original text was published but eight years ago, the author has realized for some time that it was already out-of-date in certain respects. He has been somewhat amazed, in making a careful check of the book, to find how many of its statements have become questionable in the light of modern research. To the uninitiated, the subject of Anatomy is one that does not change from one generation to the next. This is true, of course, to a certain extent only. While the main facts of Anatomy remain unchanged through the years, certain concepts concerning the homologies of structures may be shown to be wrong as the result of a single investigation. For example: while the endostyle occupies the same position in the pharynx of *Amphioxus* that it did when the author studied Comparative Anatomy in his college days, its homology to the thyroid gland now seems doubtful as a result of recent studies in embryology. Many other concepts that the author has taught for over a quarter of a century now seem to be equally questionable. A number of such cases are briefly considered and discussed in the Revised Edition.

During the revision of this text the author has become deeply indebted to many persons, some known but many who must remain nameless. He is especially grateful to the many users of the original book, most of whom are unknown to him, who have sent to the publishers helpful suggestions and criticisms; to the many hundreds of students of his own classes who, as patient "guinea pigs" have had the original text tried out on them; to Professor Curtis L. Weathers, a colleague of many years, who has never failed to offer helpful advice and encouragement; to Agnes E. Ream, a former student, who has unselfishly devoted much time and effort to the preparation of the manuscript, the checking and labeling of figures, and the preparation of the index; to Mary H. Fushi, a talented artist with no previous experience in scientific drawing, who has redrawn many of the figures with skill and accuracy; to Professor Alfred F. Huettner for his gracious permission to use a number of original drawings from his *Fundamentals of Comparative Embryology of the Vertebrates;* and, finally, to The Macmillan Company, for their generous coöperation in every effort to make this Revised Edition much better than the original.

HAROLD M. MESSER

Baker Hill, Newbury
New Hampshire

Preface to First Edition

In the preparation of this text it has been the intent of the author to present an adequate but not too detailed account of vertebrate anatomy. After a number of years' experience in teaching a one-semester course in the subject, he has come to favor more and more, for the required text, a book containing a minimum amount of material. This may be supplemented in various ways: as by occasional assigned readings in larger and more comprehensive reference books, or by the expansion and explanation of the subject matter, when such treatment seems desirable, in the formal lectures.

The author lays no claim to originality for the details and long-known facts of vertebrate anatomy herein assembled. If he has been fortunate enough to have selected from a mass of details, those most essential, and if, in their presentation, he has been able to arrange these facts in such a way as to arouse the interest of the student, he will be quite content.

The manner of treatment, by systems rather than by types, has been followed in the author's classes at Long Island University for a number of years, and has proved to be much more satisfactory than the older type-study method. By following this systemic method it has been possible to bring about a much closer correlation of textbook assignments, formal lectures, and laboratory exercises. Such correlation seems especially desirable in a short course which has to cover such a large field of subject matter.

The needs of two groups of students, the pre-professional and the biology major, have been kept in mind in the preparation of this text. For the pre-professional student, the study of vertebrate anatomy should serve as a background that will make subsequent study of human anatomy less difficult and more significant. On the other hand, the student who is interested in some particular phase of Biology needs a knowledge of the fundamentals of vertebrate anatomy before continuing in a more specialized field.

The author wishes to acknowledge his debt of gratitude to several past and present members of the Department of Biology of Long Island University for their assistance in reading various portions of the manuscript and for their many valued criticisms and helpful suggestions. Among these are Dr. H. Randolph Halsey who read the first four chapters and Dr. R. E. Bowen and Professor C. L. Weathers who read the entire manuscript. Although many of their suggestions have been incorporated in the text the author naturally assumes sole responsibility for any errors that may still be present. The assistance of Miss Alice M. Diehl, in critically reading the entire manuscript, and of Miss Eleanor Martinson in the tedious labor involved in the preparation of the manuscript for the press, is also gratefully acknowledged.

For permission to reproduce illustrations, acknowledgments are made in the accompanying legends. In this connection I am especially grateful to Henry Holt and Company, and Miss Mary W. Kingsley for permitting the use of an unusually large number of figures; to the American Museum of Natural History and the New York Zoological Society for the use of numerous photographs; and to The Macmillan Company for their generous coöperation in all matters concerning illustrations.

An earnest effort has been made to obtain a relatively large number of original drawings. In their preparation a number of former students have been most helpful. Among these should be mentioned Miss Julia Scarsten, Bernard Post, and William Zenvener. Girard Craft has assisted in redrawing several illustrations from other textbooks. The great majority of original and redrawn illustrations, however, are the work of Miss Frances Maltese. The author finds it especially difficult to adequately express his obligations to this student, for her cheerful contributions of time, a never-failing interest, and a very real ability in the making of scientific drawings.

Finally the author wishes to express his sincere appreciation to the many students of the past who have worked with him in the classroom and the laboratory, and whose interest and enthusiasm have served as incentives for the preparation of this text. If these pages serve to awaken in the students of the present and future a similar interest in the subject of vertebrate anatomy, the author will feel that his efforts have not been in vain.

HAROLD MADISON MESSER

Baldwin, Long Island
June, 1938

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An Introduction to
VERTEBRATE ANATOMY

I. *Introduction*

DEFINITIONS OF TERMS

The term Anatomy may be defined as the study or science of structure or form. The term itself comes from the Greek meaning "to cut up." Anatomy then means literally a knowledge of structure gained by the method of dissecting. In a broader sense it is often applied to the study of surface structure and body form. The term External Anatomy is often used in contrast to Internal Anatomy. Originally used in connection with the study of the larger divisions of the body such as the systems and organs, the scope of the term Anatomy was greatly widened by improvement of the microscope. This made possible the study of the finer details of structure of the organs. It became necessary from that time on to distinguish between Gross Anatomy and Microscopic Anatomy. Microscopic Anatomy may be still further divided into Histology, the study of tissues; Cytology, the study of cells; and Pathology, the study of diseased tissues.

It is possible also to study Anatomy with respect to the changes which take place during the development and growth of an individual organism. Such a study may be called Developmental Anatomy, with the term Embryology being used in reference to the study of the development of a given animal from the time of fertilization of the egg to the attainment of sexual maturity. In actual practice in the classroom, the field of Embryology is usually limited to the period of development extending from the fertilization of the egg to the time of hatching. The term Ontogeny is often used in referring to the development of an individual through its entire lifetime. Phylogeny, on the other hand, deals with the evolutionary changes taking place during the development of a given species through the lower forms of life.

Comparative Anatomy is the study of the morphology of a given group of organisms by comparing the structures in the various members of the group. Such a study obviously could include Histology, Embryology, and Ontogeny and would throw a great deal of light on Phylogeny.

It is difficult to study the form and structure of a given animal without paying some attention to function. The study of function is known as Physiology. The details of structure of an organ often have little meaning to us unless we know what part each plays in the functioning of the whole organ. The same statement could be made with reference to the study of an animal as a whole. The functions of the different organs of a given system and the role of the different systems in relation to one another often aid in our understanding of the anatomy of those structures.

In our study of Vertebrate Anatomy by the comparative method, the terms Homology and Analogy will be used frequently. It will be stated that a certain organ in one animal is homologous or analogous to a given organ in another animal, or that one organ is the homologue or analogue of another. Homologous organs are those which have the same kind of an evolutionary and embryonic origin and which are alike or similar in structure. Organs are said to be analogous when they have a like function.

Examples of homologous organs are the paired limbs of terrestrial animals and the paired fins of fishes. These also would be considered analogous since they have a similar function in connection with locomotion. The wings of a bird and the wings of an insect are analogous organs as they are used for the same function. They are, however, not homologous since they have very different origins. The study of homologies is obviously an important part of the whole field of Comparative Anatomy.

A great deal of our present knowledge of the phylogeny of the vertebrates has been obtained through the study of fossils. This study is known as Paleontology. Much information concerning the relations between living animals has come from these studies of animals that have long been extinct.

PLAN OF STUDY

Various methods or plans of study may be followed in the presentation of a course in the Comparative Anatomy of a given group of animals. Among these, two may be mentioned as being the most important and most widely used. These may be called the *Type-study* method and the *Systemic* method. The former plan is perhaps the older one, and, as followed in the study of Vertebrate Anatomy, consists of the complete study of a typical representative of each major group, or class, of the vertebrates. These types are studied in a logical order, that is, the simpler or lower forms first. The systemic plan presents the comparative study of anatomy by organ systems rather than by types. Under such a plan the various systems of different representative animals are considered, one after the other, beginning often with the integument. This plan has been followed perhaps to a greater extent in textbooks than it has in laboratory instruction. It can be followed satisfactorily however, in the laboratory by using a few representative animals, such as a fish, an amphibian, and a mammal. This text treats of Vertebrate Anatomy according to the systemic plan.

In studying the anatomy of a single larger animal, such as a cat or man, the *regional* method of study is often followed for greater convenience. Under this method the body is divided into various regions such as the head and neck, the thorax, the abdomen, and the two pairs of appendages. The organs in these various regions are studied separately and in detail.

TERMS OF DIRECTION OR RELATION

In the study of anatomy it is often necessary to use certain terms which indicate direction or the relation of a given structure to the long axis of the body. Several of the most commonly used terms of this character are as follows:

Anterior — toward the head, in front of
Posterior — toward the tail, in back of
Cranial — toward the head (cranium)
Caudal — toward the tail

Dorsal — toward the back of the animal
Ventral — toward the belly of the animal
Medial — toward the median line
Lateral — away from the median line
Proximal — nearer the long axis of the body, as in an appendage
Distal — farther away from the long axis, as in an appendage
Peripheral — nearest the surface

Most of the above terms may be used as adverbs denoting direction of movement by using the ending *ad*, instead of *al.*

These terms as used here apply to a typical quadrupedal animal such as a cat. Their use is somewhat confusing when referring to a bipedal animal such as man. The terms Superior and Inferior for example are often used instead of Anterior and Posterior.

PLANES AND SECTIONS

Various imaginary planes may be referred to in the study of anatomy. The body of an animal may be cut into sections through these planes. *Longitudinal sections* are those which are cut parallel to the long axis of the body, that is from the anterior to the posterior end. Such sections may be made in a great variety of planes but those of greatest importance to us are cut in either a horizontal or a vertical plane. A vertical section in the exact median line, dividing the body of an animal into right and left halves, is a *Sagittal section.* The term *parasagittal* may be applied to any longitudinal section parallel to the sagittal. A *Coronal* or *Frontal section* is made in the horizontal plane, at right angles to the sagittal, and divides the body into dorsal and ventral parts. *Transverse* or *Cross sections* pass through the body at right angles to the long axis and divide it into anterior and posterior portions.

II. The Chordates

Although this text is chiefly concerned with the details of Vertebrate Anatomy, it is important to remember that the term "vertebrate" includes only a portion of those animals which are grouped together in one of the major subdivisions of the animal kingdom, the phylum Chordata. When we somewhat loosely divide animals into vertebrates and invertebrates, we fail to take into account a number of forms such as *Balanoglossus*, the Tunicates, and *Amphioxus*. These and their relatives are also Chordates, and have certain characteristics in common with the vertebrates.. It would be more accurate, perhaps, if such a division is desirable to speak of Chordates and Non-chordates, instead of Vertebrates and Invertebrates.

CHORDATE CHARACTERISTICS

Of the many structures characteristic of the more important members of the phylum, only three are present in all its representatives. These are a notochord; a single, dorsal, tubular nerve cord; and a series of pharyngeal pouches. These three structures are present in all Chordates at some period of their life history. In the higher vertebrates the notochord and the pharyngeal pouches are embryonic structures which do not persist in the adult.

The Notochord

The notochord (Fig. 1) is a stiff supporting rod of vacuolated cells having a somewhat variable origin in different forms and in its different regions. The anterior end may be derived directly from the endoderm of the dorsal portion of the alimentary canal (Fig. 2). Its more posterior portions, in many vertebrates, are closely associated with the mesoderm, apparently originating from the undifferentiated cells in the region of the primitive streak. It forms an axial support for the body, and is present in all chordates in the embryo. The notochord is surrounded by sheaths of connective tissue (Fig. 1). In some chordates it remains unmodified in the adult as the permanent skeletal axis; in others it becomes modified by the addition of cartilaginous neural processes; and in the higher vertebrates it is entirely replaced by cartilaginous or bony vertebrae.

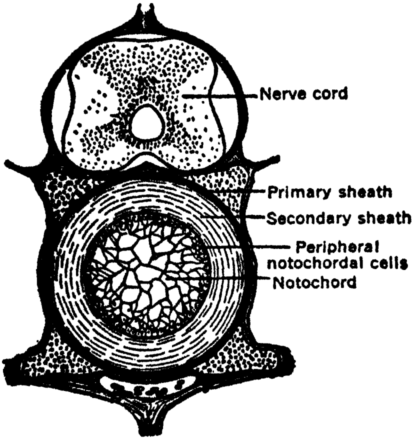

Fig. 1. Notochord of a young dogfish. Cross section showing nerve cord and sheaths of notochord. (From Hegner, *College Zoölogy,* after Burdon, by permission of The Macmillan Company, publishers.)

The Nerve Cord

The nerve cord of the chordates is a single, hollow tube located dorsal to the alimentary canal and to the notochord. Developing in the embryo from the outer layer of cells (ectoderm) along the dorsal surface, it later becomes buried below the surface for greater protection (Fig. 3). By a process known as invagination, a groove appears along the middorsal surface. This groove, by the rapid growth of cells along its edges, pushes deeper and deeper into the underlying tissues. Eventually, the side walls meet dorsally along the median line, thus forming a hollow tube. Later this tube becomes entirely detached from the outer layers, other tissues growing in between.

The nerve cord thus formed differs radically from that of a typical non-chordate, which develops from a double row of ectodermal cells along the ventral surface. These eventually split off from the external layer, forming the ventral, double

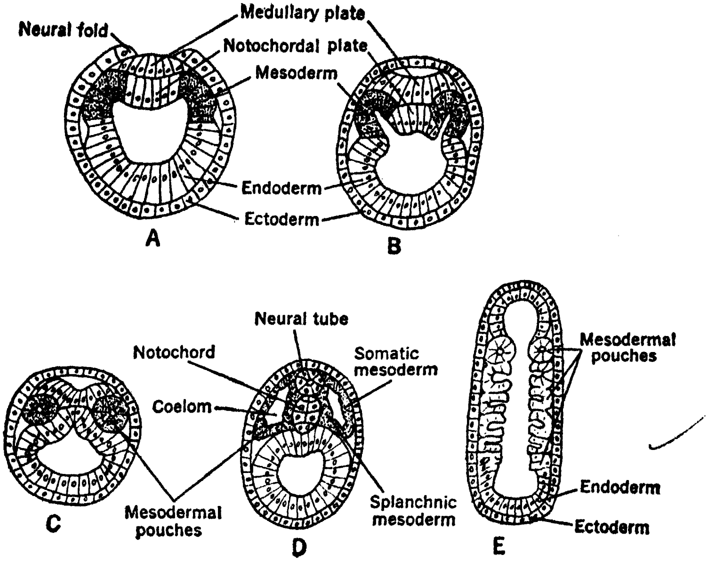

Fig. 2. Diagrams showing formation of the neural tube, notochord, and mesoderm in *Amphioxus*. A–D, cross sections; E, frontal section. (Redrawn from Walter, *Biology of the Vertebrates*, after Hatschek, by permission of The Macmillan Company, publishers.)

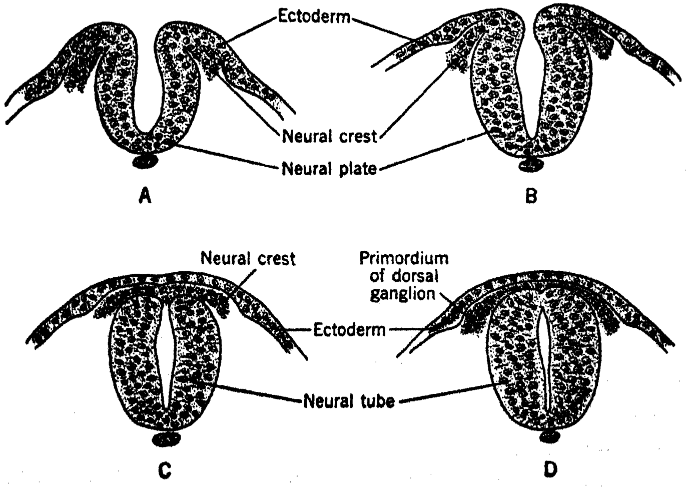

Fig. 3. Drawing (x 135) showing closure of the neural tube and formation of the neural crest. From pig embryos of: A, 8 somites; B, 10 somites; C, 11 somites; D, 13 somites. (Redrawn from B. Patten, *Embryology of the Pig.* Copyright Blakiston Co., publishers.)

and solid nerve cord characteristic of these organisms. This splitting-off process is known as delamination.

The Pharyngeal Pouches

This term is applied to the segmentally arranged pockets which push out as lateral diverticula from the walls of the pharynx (Fig. 4). In the aquatic chordates these meet with similar pockets, the branchial grooves or furrows, which push inwardly from the external surface. The intervening walls eventually break through, forming the gill slits. On the sides of these gill slits, the gill filaments, the fundamental units of the respiratory system, later develop.

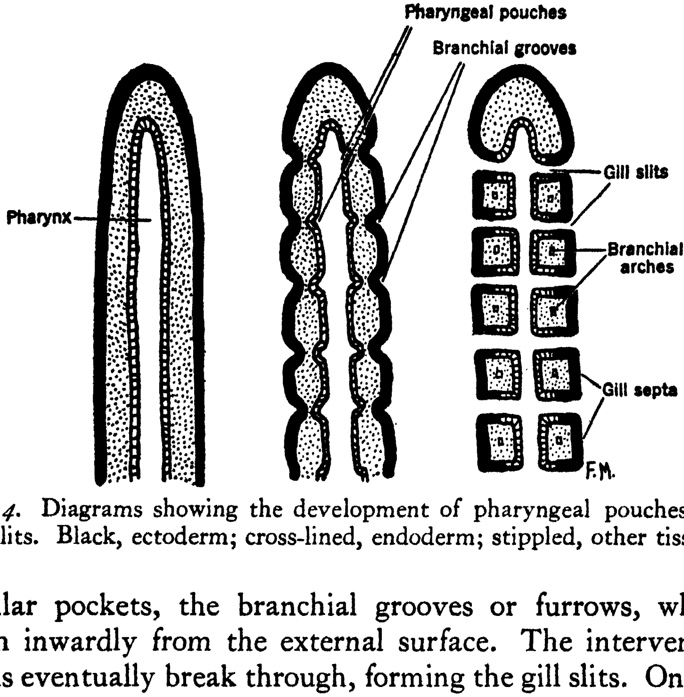

Fig. 4. Diagrams showing the development of pharyngeal pouches and gill slits. Black, ectoderm; cross-lined, endoderm; stippled, other tissues.

Although the gills are replaced by lungs in the land-living chordates, portions of this pharyngeal breathing device appear as transitory structures in the embryo. The pharyngeal pouches, at least, appear at some time during the embryonic life of all chordates, and portions of them play a part in the formation of other structures, such as some of the ductless glands (Fig. 395) of the adult. Gills never develop in relation to these pouches in forms above the amphibians.

OTHER CHORDATE FEATURES

The three characteristics just mentioned are found, as has been stated, in all chordates at some time during their lives. They are distinguishing characteristics none of which appear in the non-chordates.

In addition to these, a number of other features appearing in the lower phyla are retained in the chordates to a greater or a lesser degree. Among these may be mentioned bilateral symmetry; coelomic or body cavities; decreasing metamerism; and increasing cephalization.

Bilateral Symmetry

The members of the higher non-chordate phyla are said to be bilaterally symmetrical. This same general plan of body symmetry is seen in the chordates. To possess bilateral symmetry, the body of an animal must be so organized that it is possible to pass one plane, and one plane only, through the body in such a manner that the two parts thus separated are alike. Such a plane, called a sagittal plane, must be passed longitudinally (through the long axis of the body) from the middorsal to the midventral line. If an animal possessing bilateral symmetry is hemisected along this plane, the two halves are said to be mirror images of each other.

Although probably no animal possesses absolutely ideal bilateral symmetry, the higher non-chordates and the chordates approximate such a condition. The term is a convenient one to use in contrast to other types of symmetry such as spherical and radial symmetry, as seen in lower forms of animal life.

The Coelom

The coelom, or body cavity, appears quite early in non-chordate history (Fig. 5). Originally, the coelom consists of a series of cavities corresponding to the body segments, and separated from one another by transverse membranes. From this simple condition, there is a tendency toward the elimination of these partitions, resulting in a decrease in the number of cavities. This tendency continues in the chordates, the members of the highest class (Mammalia) possessing typically a coelom divided into but two main parts, the thoracic and abdominal cavities.

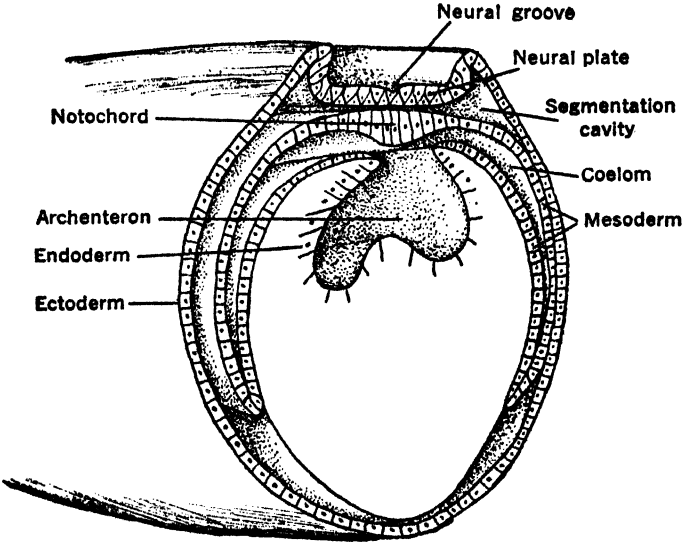

Fig. 5. Diagram of a cross section of an amphibian showing the developing nerve cord, notochord and mesodermal pouch. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

Metamerism

It was previously stated that the chordates show decreasing evidences of metamerism, or segmentation. It will be recalled that this principle of body organization is first seen in the phylum Annelida, and it is in this same group that it reaches its highest development. The typical annelid consists of a series of segments, or metameres, which are essentially similar, both internally and externally, and each of which possesses a pair of appendages.

Among the arthropods this body plan is still more or less apparent externally, but is much less evident in the arrangement of the internal structures. The more anterior segments have become indistinguishable, having united to form a head. This is followed by a group of the centrally located metameres which form the thorax. The abdomen, consisting of the posterior metameres, retains more external evidences of this primitive arrangement. In such a form as the lobster, for example, the number of abdominal segments is quite apparent, while that of the head and thorax can be determined only by counting the number of pairs of appendages, which, although highly modified, are retained. Internal evidences of metamerism are very much obscured in the arthropods by the substitution of blood sinuses for the coelom.

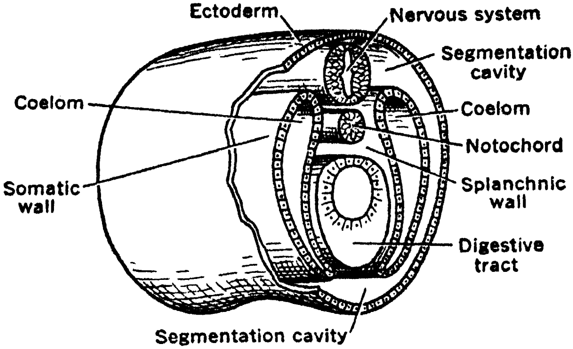

Fig. 6. Stereogram of the anterior end of a vertebrate, showing the coelomic pouches; at a later stage of development than in Fig. 5. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

Among the chordates, on the other hand, it is chiefly in the internal structures that metamerism is still in evidence. The myomeres or muscle segments are seen in their primitive condition in the lower vertebrates, and in the embryos of the higher ones. The kidney tubules, the vertebrae, the spinal nerves, and some of the paired blood vessels of many higher vertebrates are among the remaining evidences of metamerism. The number of appendages has been very much reduced, and can no longer be used as an indication of the number of segments present. In no chordate are there more than two pairs of paired appendages.

Cephalization

A condensation of the anterior segments to form a head has been noted in the arthropods among the non-chordates.

The head consists very largely of the brain, the special sense organs, and supporting or protecting structures. This tendency toward localization of the brain, the sense organs, and the mouth at the anterior end of the body is known as

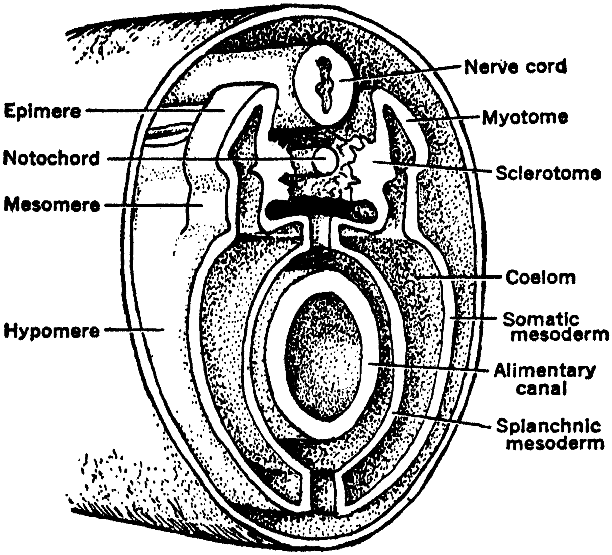

Fig. 7. Diagram of a cross section of a developing vertebrate, showing the parts of the mesodermal segments. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

cephalization. Beginning in forms lower than the arthropods, it reaches its highest manifestation in the higher classes of the chordates. ✓

CLASSIFICATION OF THE CHORDATES

Although it is not the purpose of this text to emphasize classification, it is essential that the main divisions of the phylum be known and their relationships understood before the anatomy of the different groups can be intelligently compared. It is realized that the system adopted in the following chapters will not be satisfactory to all taxonomists. It has been chosen because of its simplicity, and because it seems adequate for the purpose of this book.

The Subphyla

It is convenient to divide the phylum Chordata into two divisions or subphyla; namely, Protochordata and Vertebrata. The former group includes a variety of dissimilar animals, which are alike in at least one respect; namely, that they possess at some time during their lives a supporting structure, the notochord. This may or may not persist in the adult. If it does remain, it is never modified by the addition of vertebral elements. These non-vertebrate chordates will be considered briefly in this text, as necessary stepping-stones to a clear understanding of vertebrate anatomy.

The subphylum Vertebrata includes all chordates in which the notochord in the adult has been either modified by the addition of segmentally arranged cartilages, which develop in the connective tissue surrounding it, or entirely replaced by a segmented column made up of cartilaginous or bony units, the vertebrae.

The Classes

These two large groups are further subdivided into a number of classes as indicated below. The further division into smaller groups, as well as the characteristics upon which such division is based, will be described in the two following chapters.

- Subphylum — PROTOCHORDATA [1]
  - Class — Hemichorda
  - Class — Urochorda
  - Class — Cephalochorda
- Subphylum — VERTEBRATA
  - Class — Agnatha
  - Class — Chondrichthyes
  - Class — Osteichthyes
  - Class — Amphibia
  - Class — Reptilia
  - Class — Aves
  - Class — Mammalia

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[1] The three groups here described as classes of the subphylum Protochordata are often given the rank of subphyla.

SUMMARY

All Vertebrates are Chordates but not all Chordates are Vertebrates. Further, all Non-chordates are Invertebrates but not all Invertebrates are Non-chordates. The three distinctive Chordate characteristics are the Notochord, the single, dorsal, tubular Nerve Cord, and Pharyngeal Pouches. Other features associated with Chordate organization are Bilateral Symmetry, the Coelom, Metamerism, and Cephalization.

The phylum Chordata is divided into two subphyla, Protochordata and Vertebrata. The subphylum Protochordata is further subdivided into three classes, Hemichorda, Urochorda, and Cephalochorda. The subphylum Vertebrata includes seven classes: Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia.

III. *The Protochordates*

This subphylum contains a large number of widely dissimilar forms which at first sight seem to have little in common with the vertebrates, or even with one another. A closer study, however, reveals the fact that all of its members possess at some time during their life the three characteristics which have been mentioned previously as essentially chordate; namely, a notochord, pharyngeal pouches, and a single, dorsal, tubular nerve cord. Because of this, it is impossible to place them in any of the non-chordate phyla, the members of which, in many cases, they superficially resemble. They are rather loosely held together and separated from the vertebrates by the lack of development of either cartilaginous or bony vertebral elements.

The group may be divided into three smaller divisions, which may be called classes, as follows:

Class 1 — Hemichorda
Class 2 — Urochorda
Class 3 — Cephalochorda

The characteristics of these three classes and the structure of at least one typical representative of each class will suffice for the purpose of this text.

HEMICHORDA

As the name implies, this class includes those types in which the notochord is very short compared to the length of the body as a whole. Perhaps the best-known member of this group is *Balanoglossus* (Fig. 8), an organism which resembles, in many respects, a segmented worm. Some biologists, although recognizing their prechordate tendencies, still consider these forms to be invertebrates.

Balanoglossus

Balanoglossus lives in the shallow waters of the sea, where it burrows in the sandy or muddy bottom. There are several species, which range in size from a few centimeters to two or more meters in length. The body is divided into three main regions: an anterior proboscis; a narrow encircling fold, the collar; and the long trunk, which is in general cylindrical in shape except for two flattened surfaces on opposite sides.

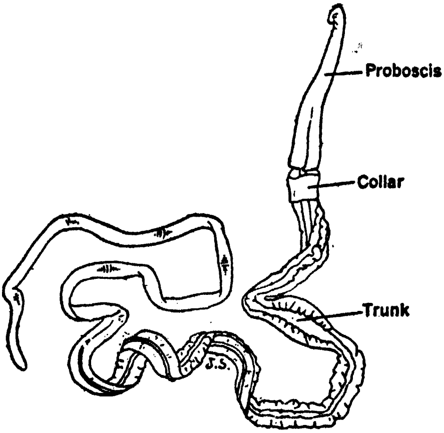


Fig. 8. A hemichordate, *Balanoglossus.*

The hollow proboscis (Fig. 9), which is used in burrowing, has muscular walls. Its cavity opens to the outside by means of a small opening, the proboscis pore, located beneath the anterior edge of the collar. The collar also is muscular and hollow, and its cavity opens to the exterior by a pair of collar pores which communicate with the gill slits.

The mouth is located at the base of the collar opposite the proboscis pore. On the dorsal surface of the anterior region

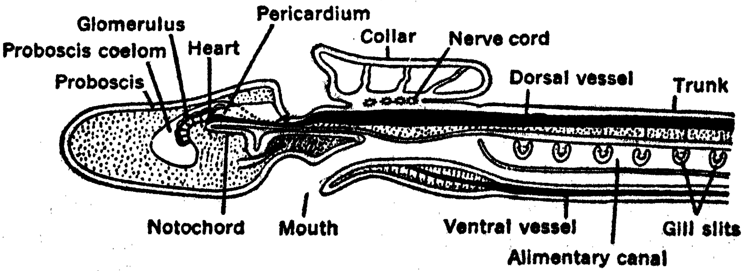


Fig. 9. Glossobalanus. Longitudinal vertical section through the middle line. Enlarged. (From Hegner, *College Zoölogy*, after MacBride, by permission of The Macmillan Company, publishers.)

of the trunk is a double row of small gill slits, located in longitudinal furrows. These open internally into the anterior part of the alimentary canal, and are supported by bars. The remainder of the alimentary canal is a simple straight tube leading to the anus, which is located terminally. In the middle region of the canal, paired hepatic caeca are given off as diverticula, which bulge outward to form prominences visible externally.

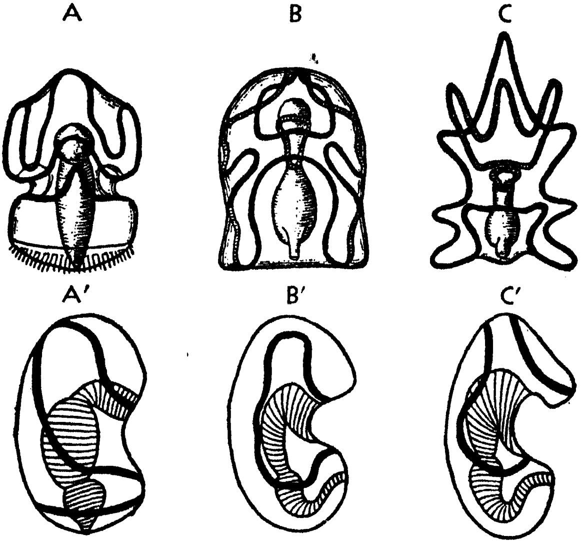


Fig. 10. Comparison of *Tornaria* larva with larval echinoderms. Main ciliated bands in black, lesser systems cross-lined. Ventral aspect: A, *Tornaria;* B, *Auricularia* (sea-cucumber); C, *Bipinnaria* (starfish). Lateral view: A′, *Tornaria;* B′, *Auricularia;* C′, *Bipinnaria.* (From Lull, *Organic Evolution,* after Wilder, by permission of The Macmillan Company, publishers.)

A hollow diverticulum from the anterior part of the alimentary canal extends for a short distance into the dorsal portion of the proboscis. Because of some embryological evidence, this structure has been thought to be homologous to the notochord of the chordates. Such a belief is now considered somewhat doubtful.

The nerve cord consists of dorsal and ventral strands of nerve tissue which extend throughout the length of the body. The two strands are connected by commissures at the base of the collar. The only part of the nerve cord to resemble the chordate type in being tubular is a short portion of the dorsal cord in the collar region.

The larva of *Balanoglossus*, known as the *Tornaria* larva, is strikingly similar to the *Auricularia* larva of the sea cucumber and to the *Bipinnaria* larva of the starfish (Fig. 10). This resemblance suggests a possible relationship between the two groups, Hemichorda and Echinodermata. The implications of this possible relationship are considered more fully in the concluding chapter of this text.

Other Examples of the Class

Among the best-known forms which are closely related to *Balanoglossus* may be mentioned *Cephalodiscus* and *Rhabdopleura*. These are sessile forms whose chief claim to relationship to *Balanoglossus* lies in the possession of a notochord, which is essentially similar in structure and in its relation to other organs.

UROCHORDA

This class includes the tunicates, or ascidians, and a number of closely allied forms, all of which are marine (Fig. 11). The name of the class refers to the fact that the notochord is confined to the tail region. This group also shows little apparent relationship to the vertebrates. Many of the urochordates pass through a series of remarkable changes during their life history (Fig. 12). It is during the larval stage that their affinities to the other chordates are revealed. The notochord, for example, is found only in the larva in a majority of the representatives. The adults are often sessile, while the larvae are all free-swimming. Many of the group form colonies, either stationary or free-swimming, and in some a definite alternation of generations occurs.

The body is enclosed in a test, or tunic, composed of tunicin, a fact which has given rise to the term Tunicata, often used as the name of the class. Tunicin is a material

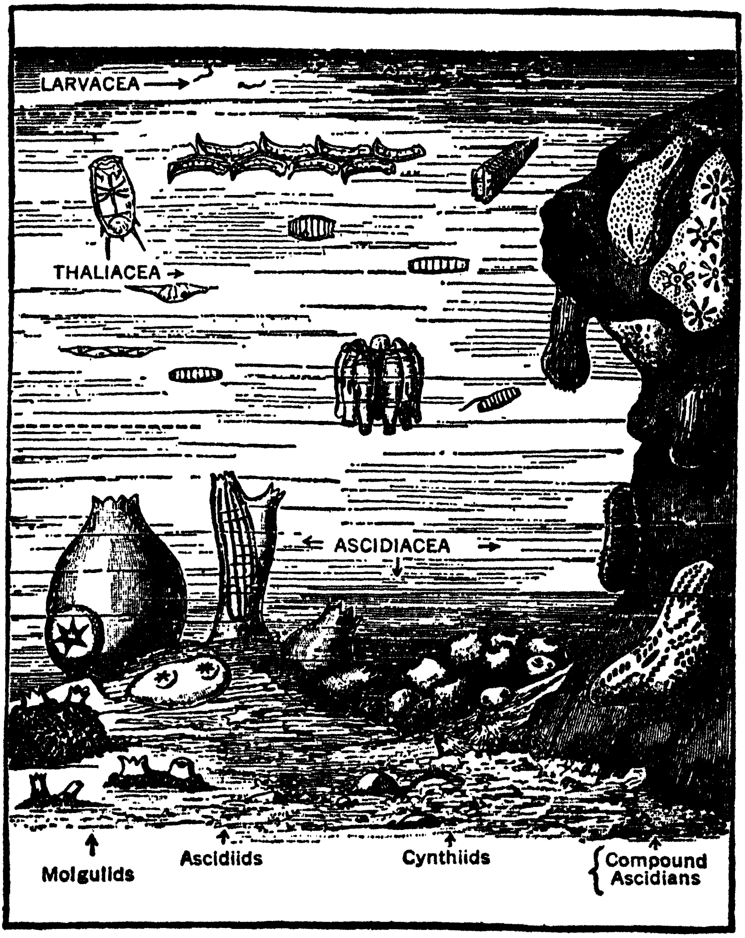


Fig. 11. Sketch of the chief kinds of tunicates found in the sea showing their distribution and habits. The dotted lines on the left indicate the life zones of the sea: the surface of pelagic zone; the middle zone; and the sea-bottom zone. (From Newman, *The Phylum Chordata*, after Herdman in the Cambridge Natural History, Vol. VII, by permission of The Macmillan Company, publishers.)

somewhat resembling cellulose, which is so common in plant tissues. ✓

Ciona

Ciona may be described as a typical tunicate. During the larval stage, this animal is a free-swimming organism, somewhat resembling a tadpole. It has a definite notochord; a neural tube which enlarges anteriorly to form a vesicle which has been considered to be the forerunner of the vertebrate brain; and gill slits which connect the cavity of the pharynx

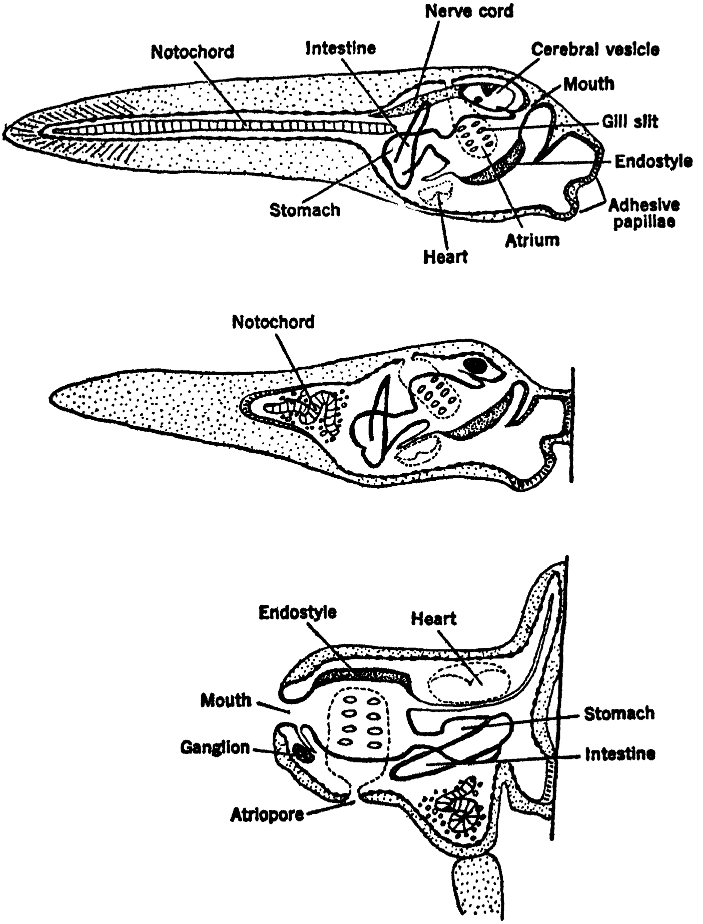


Fig. 12. Metamorphosis of ascidian larva. (Redrawn from Newman, *The Phylum Chordata*, after Seeliger, by permission of The Macmillan Company, publishers.)

with the exterior. After a short period, the free-swimming larva attaches itself to some object; and, during what may be called a retrogressive metamorphosis, the tail, the notochord, the neural tube, and other typical chordate features disappear.

The adult *Ciona* is a sessile form having little in common with the typical chordates. The outer transparent covering of the body is known as a tunic, or test. At the extreme free end is an orifice, the oral opening; and on one side of the animal, a short distance below this, is a second opening, the atriopore. Suspended within the test is the soft-bodied organism, surrounded by the body wall, or mantle, which is attached to the test at two places only, around the oral and the atrial openings. (For the structure of a similar form see Fig. 13.) Currents of water enter through the oral opening and pass out through the atriopore. The oral opening, or mouth, opens into a large cavity, the pharynx, the walls of which contain many slitlike openings, the gill slits. These lead to a surrounding cavity, the atrium, and through this

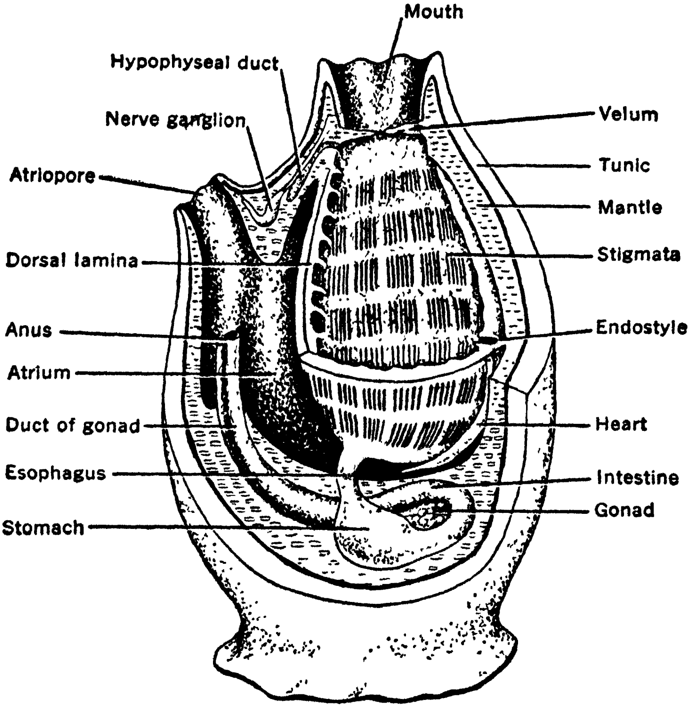


Fig. 13. Internal anatomy of a typical ascidian. (From Newman, *The Phylum Chordata*, modified after Hertwig, by permission of The Macmillan Company, publishers.)

cavity are in communication with the exterior by way of the atriopore.

The pharynx leads directly into the esophagus, which is followed by a curved region, the stomach. The alimentary canal then continues as the intestine to the anus, which opens within the atrial cavity.

The circulatory system is well developed. It includes a pulsating, saccular heart, a series of quite definite channels or sinuses, and other larger and less definite spaces. Among the more definite channels are dorsal and ventral vessels in the pharyngeal region and vessels which supply the organs of the digestive system, the gonads and the mantle. Many small vessels pass around the pharynx, between the gill slits, and connect the dorsal and ventral vessels.

The nervous system is very simple, consisting of a single ganglion lying in the angle between the oral and atrial openings.

The gonads lie near the stomach, and are provided with ducts which open within the atrial cavity near the anus.

Through the transparent tunic may be seen longitudinal muscle strands and also a transverse ring of tentacles surrounding the pharynx, a short distance from the mouth. The pharynx contains an endostyle, and peripharyngeal and epipharyngeal grooves. The function of these latter structures will be described below in connection with *Amphioxus*.

Other Examples of the Class

Among other interesting members of the class may be mentioned *Molgula* (Fig. 14), *Salpa*, *Botryllus*, and *Boltenia*. *Botryllus* (Fig. 15) is a small colonial type which is commonly found growing in circular clusters on the surface of seaweed. *Boltenia* (Fig. 16) is a larger solitary tunicate, which lives attached to some submerged object by a long and slender stalk.

CEPHALOCHORDA

This relatively small class, containing about a dozen species divided between two genera, is of great interest to the student of anatomy. In the members of this class, the three structures characteristic of chordates are not only present but well developed. All possess a distinct notochord which extends throughout a greater part of the length of the animal, and which is persistent throughout the life of the individual. The nervous system consists of a hollow dorsal nerve cord which is also persistent. Paired gill slits are present, at least in the embryo. In addition to these features, the members of the group possess many others which are usually associated with the vertebrates, such as an anterior and ventral mouth, segmented muscle bundles, and a digestive gland or liver, with which are associated certain of the blood vessels to form what is known as the hepatic portal system. The best-known representative of this class is

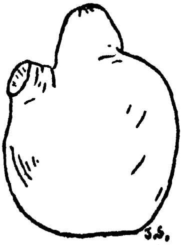


Fig. 14. A urochordate, *Molgula.*

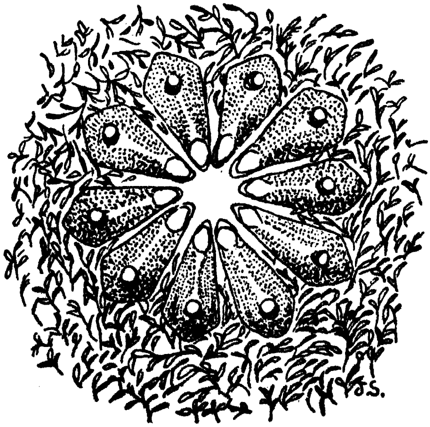


Fig. 15. A colonial tunicate, *Botryllus,* growing on seaweed.

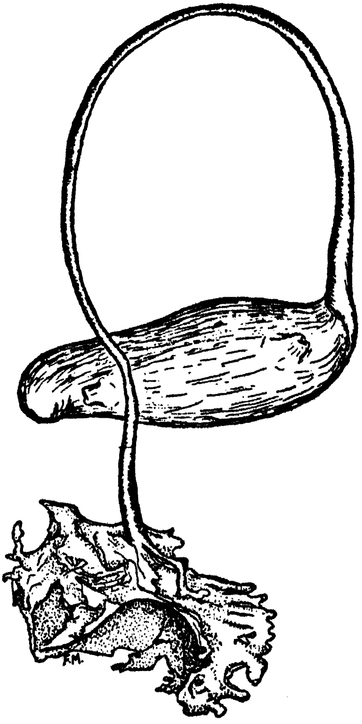


Fig. 16. A stalked tunicate, *Boltenia.*

Amphioxus, commonly called the lancelet. This form will be described in detail as a representative of the class.

Amphioxus

This small fishlike animal, which reaches a length of about two inches, is found near the shore, particularly of the Mediterranean and other temperate seas (Fig. 17). It was first described in 1778 under the name of *Limax lanceolatus* because of its resemblance to a slug. Later it was given the name of *Branchiostoma* by an Italian naturalist, Costa, who thought that the cirri were branchial structures. The name of *Amphioxus*, which was given to it a number of years later, has come to be more generally used.

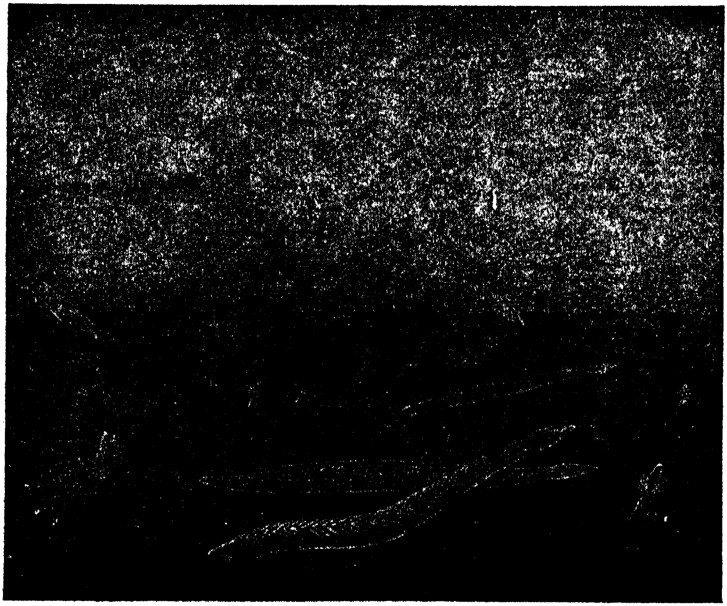


Fig. 17. A group of lancelets (*Amphioxus lanceolatus*) in normal habitat, some in the sedentary position with only the anterior end protruding from the sand burrow, one in the foreground beginning to dig a new burrow, and others swimming about in fish-like fashion. (From Newman, *The Phylum Chordata*, redrawn from indistinct photograph after Willey, by permission of The Macmillan Company, publishers.)

EXTERNALS. The body is elongated, pointed at both ends, and laterally compressed (Fig. 18). Although able to swim quite rapidly, they are more often found in burrows in the sand with only the anterior ends protruding. *Amphioxus* possesses a well-developed system of median fins. This consists of a long dorsal fin, a caudal fin around the posterior end, and a short ventral fin posterior to the atriopore. These median fins consist largely of a single fold of integument supported by a row of blocks of connective tissue. A double row of these blocks appears in the ventral fin, but in the others only a single row. On either side of the body at the latero-ventral margin is a fold of the body wall extending from near the base of the oral hood to the region of the atriopore. These are the metapleural folds (Fig. 19).

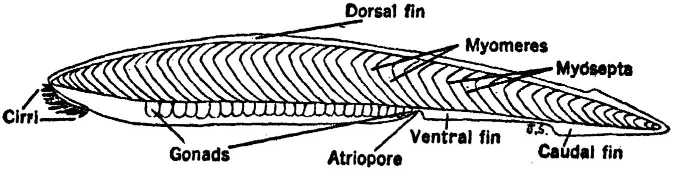


Fig. 18. Amphioxus, showing external features.

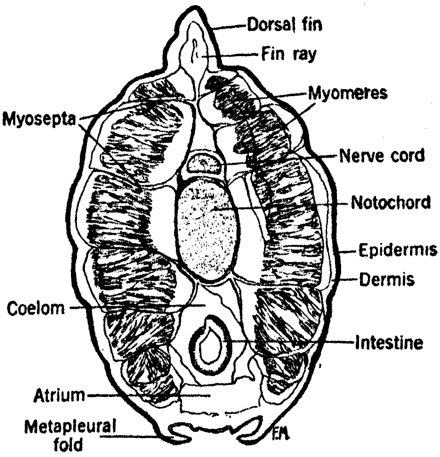


Fig. 19. Cross section of *Amphioxus*, posterior to the liver.

The integument or skin consists of two regions, an outer epidermis and an inner dermis. The epidermis consists of a single layer of cells, a condition which resembles that found in the non-chordates but not in the vertebrates. The dermis is composed largely of a kind of connective tissue. Through the skin may be seen the myomeres, or muscle segments. These appear as V-shaped segments with the apex pointing toward the anterior end.

They are not directly opposite one another, as those of one side alternate with those of the other.

The anterior end of *Amphioxus* is prolonged dorsally, forming the rostrum. Ventral to this, the anterior end is expanded, forming an oral hood. Around the edge of the hood is a fringe of fingerlike projections, the buccal cirri. Within the oral hood is a peculiar ciliated structure known as the wheel organ. This consists of several fingerlike projections attached to a horseshoe-shaped portion posteriorly. The middorsal finger is the longest and bears a longitudinal groove known as Hatschek's groove. This terminates anteriorly in Hatschek's pit. At the inner boundary of the oral hood is a transverse membrane, the velum. The mouth, which is a circular opening in this vertical membrane, bears on its rim twelve velar tentacles.

Other external openings are the atriopore on the ventral surface just anterior to the ventral fin, and the anus, located slightly to the left of the caudal fin and approximately halfway between the atriopore and the posterior end of the body.

In mature specimens the gonads may be seen externally. These are paired bodies, segmentally arranged, lying near the ventral surface between the mouth and the atriopore. As many as twenty-six pairs are present.

THE SKELETON. The chief skeletal structure of *Amphioxus* is the well-developed notochord (Fig. 20), a long rod which

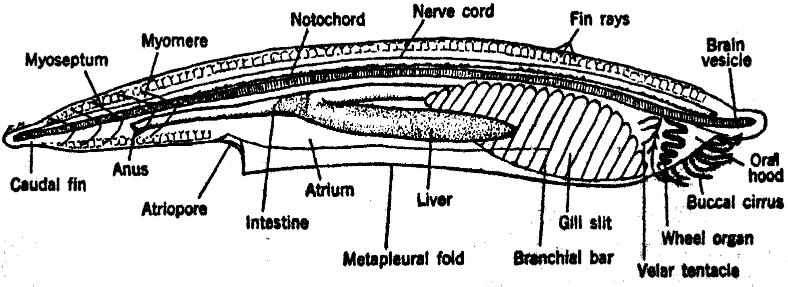


Fig. 20. Diagram showing the internal structure of *Amphioxus.*

extends from the rostrum well into the caudal fin. The notochord and nerve cord are surrounded by sheaths of connective tissue (Fig. 21). The buccal cirri are supported by a ring of jointed blocks consisting of a material resembling cartilage. From this ring a column of these elements extends into each cirrus. The pharynx is supported by a series of skeletal structures known as the gill bars. These are of two kinds, primary and secondary. The former are forked at the ventral end, while the latter end in rounded points. The adjoining bars are connected at fairly regular intervals by smaller longitudinal bars, the synapticula. The inner surface of the bars is covered with endodermal tissue, the outer surface with ectodermal tissue. The structures thus formed may be compared with the gill septa of true aquatic vertebrates. The primary bars develop first, and originally are metameric in arrangement. The secondary bars form later, pushing down as tongues between adjoining primaries and dividing each gill slit into two parts. The gill bars thus increase in number until their relation to the original body segments is lost.

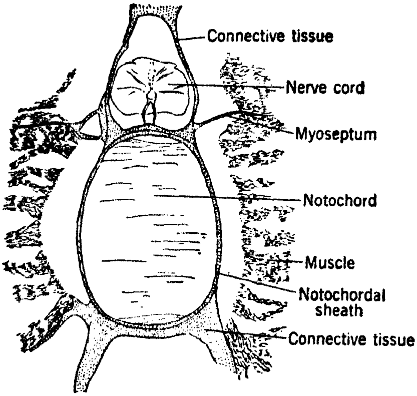


Fig. 21. Cross section through nerve cord and notochord of *Amphioxus*, enlarged, showing connective tissue sheath and septa.

Other skeletal structures which have been previously mentioned are the connective tissue blocks forming the fin rays which support the median fins.

THE MUSCLES. The muscle segments, or myomeres, are here seen in a simple and primitive condition. As described in connection with the external surface, they are V-shaped blocks separated by partitions of connective tissue, the myosepta. The myomeres of the right and left sides are not exactly opposite, but alternate with one another. Within the myomeres the muscle fibers are striated and extend longitudinally between consecutive myosepta. A narrow band of transverse muscles extends around the ventral surface.

THE DIGESTIVE SYSTEM. The mouth, which has been mentioned previously, opens directly into the pharynx, which comprises the anterior half of the alimentary canal. The pharynx is followed by a narrow portion which may be called the esophagus. This soon widens into the stomach. From this region a tubular diverticulum pushes forward into the atrium on the right side of the pharynx. This is known as the liver, although, since it produces digestive enzymes, it apparently has the function of a pancreas. Posterior to the stomach the canal narrows and continues as the intestine to the anus. A darker staining band, the iliocolic ring, may be seen in a cleared and stained specimen, around the anterior portion of the intestine.

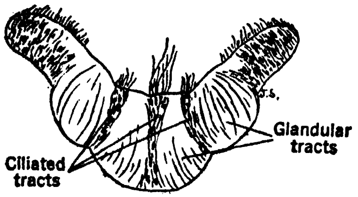


Fig. 22. Cross section through the endostyle of *Amphioxus.*

The walls of the pharynx are pierced by the gill slits, which will be described more fully in connection with the respiratory system. Along the median ventral floor of the pharynx is a groove, the endostyle, which contains four longitudinal tracts of glandular cells (Fig. 22), alternating with three tracts of ciliated cells. Opposite the endostyle in the dorsal wall is a ciliated epipharyngeal groove, which extends back to the intestine. These two grooves are connected anteriorly by the peripharyngeal grooves, which form a ciliated ring around the pharynx, a short distance within the mouth.

The feeding habits of *Amphioxus* are interesting, and will be easily remembered if the arrangement of the structures just described is understood. Water containing food material is directed toward the mouth by a current caused by the beating of cilia. Large particles are kept out by the velar tentacles and cirri, which thus serve as a strainer. A similar current posterior to the mouth, caused by the beating of the cilia of the pharyngeal walls, draws the food-laden water inward and downward to the endostyle. The glandular cells of the endostyle secrete a mucus in which particles of food become entangled. The action of the cilia on the inner surfaces of the gill bars carries the food material dorsally into the epipharyngeal groove through which it continues posteriorly into the esophagus. Food particles in the anterior part of the pharynx may reach the epipharyngeal groove by way of the peripharyngeal grooves. The cylinder of food particles and mucus thus formed is carried posteriorly through the other parts of the alimentary canal. Most of the digestion and absorption occurs in the intestine. This peculiar method of feeding, which has been called the ciliary method, is a primitive one which has not been retained in the vertebrates.

THE RESPIRATORY SYSTEM. The respiratory mechanism consists of the gill slits and the cellular membranes surrounding the gill bars, which lie between the slits. The currents of water which were described in connection with the method of feeding leave the pharynx through the gill slits and thus bathe the membranes of the gill septa. The exchange of gases, which constitutes the external phase of the respiratory process, takes place here, between the blood stream as it passes through the vessels within the gill septa and the respiratory medium (water containing oxygen) as it passes over the septa.

THE CIRCULATORY SYSTEM. Although *Amphioxus* has no heart, the system of blood vessels in other respects is fundamentally quite similar to that of the vertebrates. The blood flows posteriorly through a pair of dorsal aortae in the pharyngeal region (Fig. 23). These unite near the end of the pharynx into a single dorsal aorta which extends the length of the body dorsal to the intestine. A series of mesenteric arteries lead from this vessel (dorsal aorta), by way of the mesentery, to the capillaries of the wall of the intestine. As the blood passes through these capillaries, absorption of food materials takes place. After passing through the intestinal capillaries, the blood is collected by the subintestinal vein, which carries it anteriorly to the liver. Within the liver tissue it goes through a second set of capillaries, which is a part of the hepatic portal system. These capillaries unite to form a large vessel, the hepatic vein, which extends forward along the floor of the pharynx beneath the endostyle. This continues as the ventral aorta, a contractile vessel which serves as a functional heart and which propels the blood into the afferent branchial arteries that lead into the primary gill septa. The afferent branchials upon entering the septa divide into three vessels which run dorsally in the septa. The secondary septa contain two vessels, which are connected with those of the primary by branches which pass through the synapticula. While passing through the gill septa, the blood is aerated and continues dorsally in the vessels which are now called efferent branchials, to the paired dorsal aortae previously mentioned.

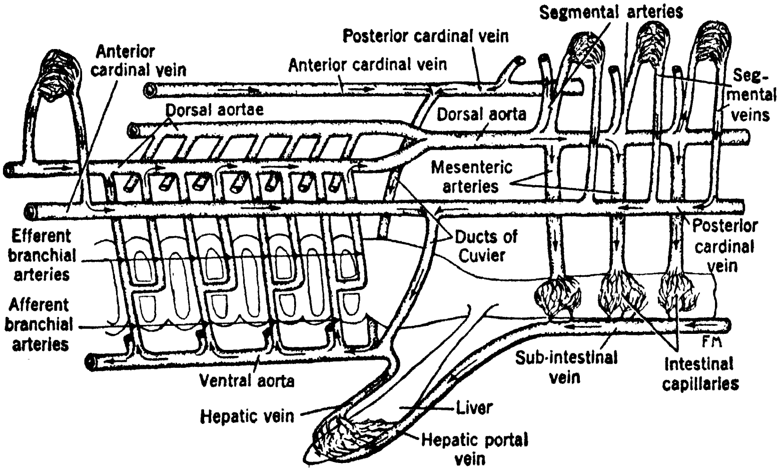


Fig. 23. Diagram of the main blood vessels of *Amphioxus*. The arrows indicate the direction of the flow of blood. (Modified after De Beer, *Vertebrate Zoölogy*, by permission of The Macmillan Company, publishers.)

The muscles of the body wall and other local structures receive blood by way of segmental arteries which branch off from the dorsal aortae within the myosepta. The blood from these vessels passes through capillaries into the segmental veins which lead into lateral vessels extending throughout the length of the body. The anterior portions of these vessels are known as anterior cardinals; the remaining portions as posterior cardinals. Just anterior to the liver the cardinals of the two sides are connected to the ventral aorta by transverse veins, the ducts of Cuvier. Blood in the anterior cardinals flows posteriorly, and in the posterior cardinals anteriorly, to the ducts of Cuvier.

It should be noted that the direction of the flow of blood, posteriorly in the dorsal vessels and anteriorly in the ventral vessels, is like that of the vertebrates, and is just the reverse of the typical non-chordate plan, as illustrated in a form like the earthworm.

THE EXCRETORY SYSTEM. The excretory system of *Amphioxus* is of the non-chordate type in that it consists of a series of paired nephridia (Fig. 24). These are bent tubes provided with flame cells and located at the sides of the dorsal region of the pharynx in close relation to the blood vessels within the gill septa. Excretory products brought to the tubules by the blood vessels are discharged into the atrial cavity, through openings in the end of the tubules. These wastes eventually leave the body through the atriopore.

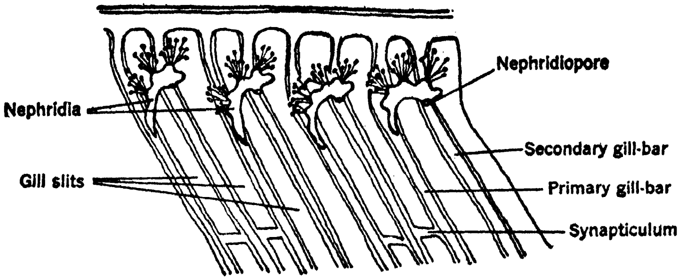


Fig. 24. Diagram of dorsal portion of the pharynx in *Amphioxus*, showing nephridia. (Redrawn from De Beer, *Vertebrate Zoölogy*, by permission of The Macmillan Company, publishers.)

THE NERVOUS SYSTEM. The central nervous system is made up of a single tubular nerve cord lying dorsal to the notochord. Although not as long as the notochord, it extends throughout a greater part of the length of the body. At its anterior end the cavity is enlarged to form the cerebral vesicle, which is the only indication of a brain. A pigment-spot at the tip of the cerebral vesicle has long been called the eyespot, although it is apparently not responsive to light. Similar pigment-spots occur more posteriorly in rows along the sides of the nerve cord. These have been shown to respond to light.

Pairs of nerves are given off from the nerve cord on each side of the body. These segmentally arranged nerves are the dorsal and ventral nerve roots. The dorsal roots transmit impulses directly from the sense organs of the skin to the nerve cord and also innervate the smooth muscles of the alimentary canal. The ventral roots are motor nerves which distribute impulses to the muscle fibers in the myomeres. The absence of ganglia on the dorsal nerve roots and the lack of a union between dorsal and ventral roots are primitive features in which *Amphioxus* differs from the vertebrates.

THE REPRODUCTIVE SYSTEM. The sexes are separate in *Amphioxus*. The gonads are paired bodies, twenty-six on either side, lying lateral to the atrium in the pharyngeal region. The germ cells, when mature, break out from the gonads and pass through the body wall into the atrium. They reach the outside by way of the atriopore. Fertilization is external.

THE ATRIUM. In the description of the respiratory system, it was mentioned that water which enters the pharynx by way of the mouth passes out through the gill slits. The gill slits of *Amphioxus* do not open directly to the outside, as they commonly do among the aquatic vertebrates, but rather into an additional cavity, the atrium. This is an interesting structure lateral and ventral to the pharynx, which apparently has no homologue in the vertebrates. As previously mentioned, this cavity opens to the outside by means of the atriopore, located just anterior to the ventral fin. On the right side of the body, the atrial cavity extends as a blind sac posterior to the atriopore, almost as far as the anus.

It should be noted that the atrium is similar to the cloaca of many vertebrates in that it receives the germ cells and the excretory wastes. It differs from a cloaca in that it also receives the respiratory medium, water, after it has passed through the gill slits.

The atrium represents a part of the external world, just ventral to the original ventral surface of the animal (Fig. 25).

This space has been enclosed laterally by the downward growth of the two longitudinal folds of body wall which have been described previously as the metapleural folds; and ventrally, by the medial growth of two horizontal folds, the epipleurs, which develop from the inner surface of the metapleurs a short distance dorsal to their ventral margins. Because of the manner of its development, the atrial cavity is lined entirely with ectoderm. It serves to protect the important structures of the pharyngeal region.

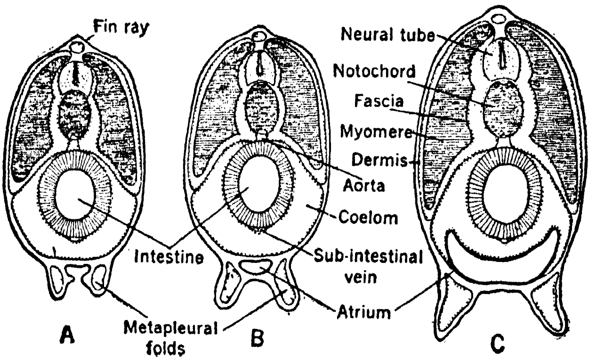


Fig. 25. Diagrammatic transverse sections of *Amphioxus* to show three stages (A, B, C) in the development of the atrium. (Adapted from Newman, *The Phylum Chordata*, after Lankester and Willey, by permission of The Macmillan Company, publishers.)

THE COELOM. The coelom of *Amphioxus* is typical posterior to the pharynx. In the pharyngeal region, there are also a pair of more or less typical dorsal coelomic cavities separated by the mesentery which suspends this portion of the alimentary canal. Below the endostyle, there is a ventral coelomic cavity known as the subendostylar coelom. These dorsal and ventral coelomic cavities are connected by narrow canals (coelomic) which extend through the primary gill septa. These coelomic canals of the primary gill septa are remains of coelomic cavities lateral to this part of the alimentary canal, which have been enclosed during the development of the gill slits.

SUMMARY

The subphylum Protochordata includes a wide variety of forms which are alike in that they possess at some time during their life a notochord, a dorsal, tubular nerve cord, and pharyngeal pouches. They differ from the vertebrates in the absence of any beginnings of vertebrae.

Balanoglossus, representing the class Hemichorda, has the chordate characteristics in the adult. In the larval stage it closely resembles an echinoderm larva.

The tunicates, on the other hand, resemble the chordates during the larval period only. The adult, as in the case of *Ciona* which is described above, is a sessile form without a notochord or tubular nerve cord.

Amphioxus, a cephalochordate, is the most important member of the subphylum, because it resembles the simpler vertebrates in so many respects. The segmental arrangement of the muscles is similar to that of the body muscles of the typical vertebrate. The respiratory system, with its gill membranes exposed to water passing out of the pharynx through gill slits, is essentially the same as in the aquatic vertebrates. The circulatory system resembles that of the vertebrates in that blood flows anteriorly in the ventral vessel and posteriorly in the dorsal vessels; but differs from it in the absence of a definite heart. The nervous system is of the vertebrate type as far as origin and development are concerned, but a definite brain and dorsal ganglia are absent. The digestive system, posterior to the pharynx, suggests that of the vertebrates, in the development of a liver diverticulum.

On the other hand, *Amphioxus* differs from the vertebrates in a number of important features. The ciliary method of feeding, involving ciliated, glandular grooves is not retained by the vertebrates. The excretory system consists of paired and metameric nephridia of the non-chordate type. The atrium and the unmodified notochord are other primitive features not retained by the vertebrates.

IV. The Vertebrates

Before beginning a comparison of the various systems of the vertebrate body as they appear in the different vertebrate classes, it is necessary to understand the relation of these different groups to one another. This involves the question of the classification of the vertebrates, and forms the material upon which the subscience of Taxonomy is based. This orderly arrangement was probably originally intended merely as a cataloguing, for the sake of convenience, of the ever-increasing number of known forms. With the development of the theory of evolution, however, taxonomy became more and more important as a method of showing the relation of one form to another.

DESCRIPTION OF TAXONOMY

It is evident that in any system of classification those forms which are listed together in the smallest group are most closely related. Similarly, any two forms in different small divisions of a larger group are less closely related. And, finally, two forms from two of the major groups of animals would show less similarity of structure and would be only distantly related.

The animal kingdom is divided into a relatively small number of major divisions, or Phyla, and these phyla are further subdivided into smaller groups known as Classes. The members of the same phylum, in general, possess in common a small number of relatively important characteristics. We have seen this illustrated in the phylum Chordata, for which we listed no more than three diagnostic features. All members of the same class, in addition to the characteristics common to the phylum, possess also other features which set them apart from the members of the other classes. In a similar manner, as we increasingly narrow and limit the size of the group under consideration, we find that its members possess a larger number of characteristics in common.

In addition to Phylum and Class, the divisions most commonly used are Order, Family, Genus, and Species. In some instances, it has been found convenient to divide these groups further into Subphyla, Subclasses, Suborders, etc.

In writing the scientific name of an animal, the genus and species only are used. It is customary to use a capital letter for beginning the name of the genus, and a small letter for that of the species. For example, the common garter snake is written thus: *Thamnophis sirtalis.* Its complete classification showing its kinship to other animals would be as follows:

Phylum — CHORDATA
Subphylum — *Vertebrata*
Class — *Reptilia*
Order — *Squamata*
Suborder — *Ophidia*
Family — *Colubridae*
Genus — *Thamnophis*
Species — *sirtalis*

THE VERTEBRATE CLASSES

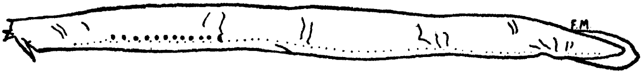
The living members of the subphylum *Vertebrata* may be divided into seven classes:

Agnatha — Lampreys and hagfishes
Chondrichthyes — Cartilaginous fishes
Osteichthyes — Bony fishes
Amphibia — Frogs, toads, salamanders
Reptilia — Snakes, turtles, lizards, crocodiles
Aves — Birds
Mammalia — Mammals

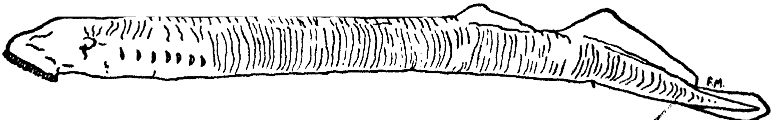
The members of these seven classes differ from the protochordates in that the notochord is either modified by the addition of cartilaginous processes or is entirely replaced in the adult by cartilaginous or bony vertebrae.

Agnatha

Characteristics. The name of the class refers to the absence of jaws. The living members of this class, commonly known as lampreys or hagfishes (Fig. 26), are placed in the order Cyclostomata. Although fishlike in many respects, as far as external appearance is concerned, they differ noticeably from the fishes in many important features. As the name implies, the cyclostomes have round mouths. The mouth opening is closed by the end of a pistonlike tongue instead of by a movable lower jaw. The cyclostomes differ in this respect from all other vertebrates. In contrast to the fishes, the integument lacks scales, there are no paired appendages, the more numerous gill slits are in the form of pouches or pockets, and there is but a single, median nasal opening.



Bdellostoma, the Pacific hagfish



Petromyzon marinus, the sea lamprey

Fig. 26. Typical cyclostomes.

The notochord, which is persistent, resembles that of *Amphioxus*, but is relatively shorter. The nerve cord is of the vertebrate type, the anterior end being modified to form a small brain. The only vertebral elements present are cartilaginous neural processes, which develop at the side of the nerve cord in the sheath of connective tissue which surrounds it. The cranium consists of a series of cartilages which protect the brain only slightly from below. These cartilages have not been satisfactorily homologized with the various elements of the skull of other vertebrates. The branchial basket, consisting of a series of cartilaginous bars and rods, supports and protects the respiratory structures in the wall of the pharynx. Here again, successful homologies have not yet been made with the branchial arches of the fishes.

The germ cells are given off into the coelom and reach the urogenital sinus through a pair of genital pores (Fig. 27).

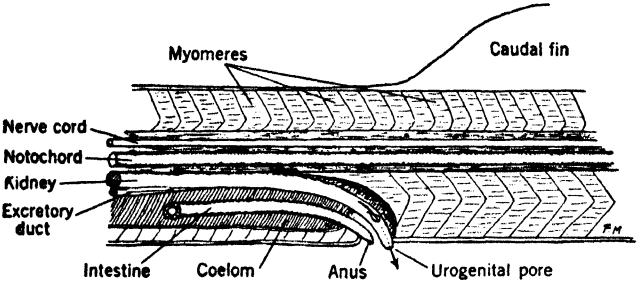


Fig. 27. Dissection of *Petromyzon* in anal region. The arrow passes from the coelom into the genital pore. (Redrawn from De Beer, *Vertebrate Zoölogy*, by permission of The Macmillan Company, publishers.)

The myomeres, the median fins, the digestive and circulatory systems are fundamentally very similar to those of the fishes.

Classification. The order Cyclostomata is commonly divided into two suborders:

1. Myxinoidea — The hagfishes, or borers
2. Petromyzontia — The lampreys

Myxinoidea. The name refers to the production of quantities of a slimy mucus, which is characteristic of this group, when disturbed. They live a semiparasitic life, boring their way into the body of fishes and eating the soft parts. The best-known genera of the group are *Bdellostoma* and *Myxine.* All species of myxinoids are marine.

Among the important characteristics of the suborder are the following:

1. The nostril is terminal and the nasal passage leads to the so-called pituitary sac, which opens into the pharynx.
2. The mouth is surrounded by four pairs of tentacles.
3. The branchial basket is poorly developed.
4. The gill slits are more numerous than in the lampreys.
5. Neural processes are present in the tail region only.

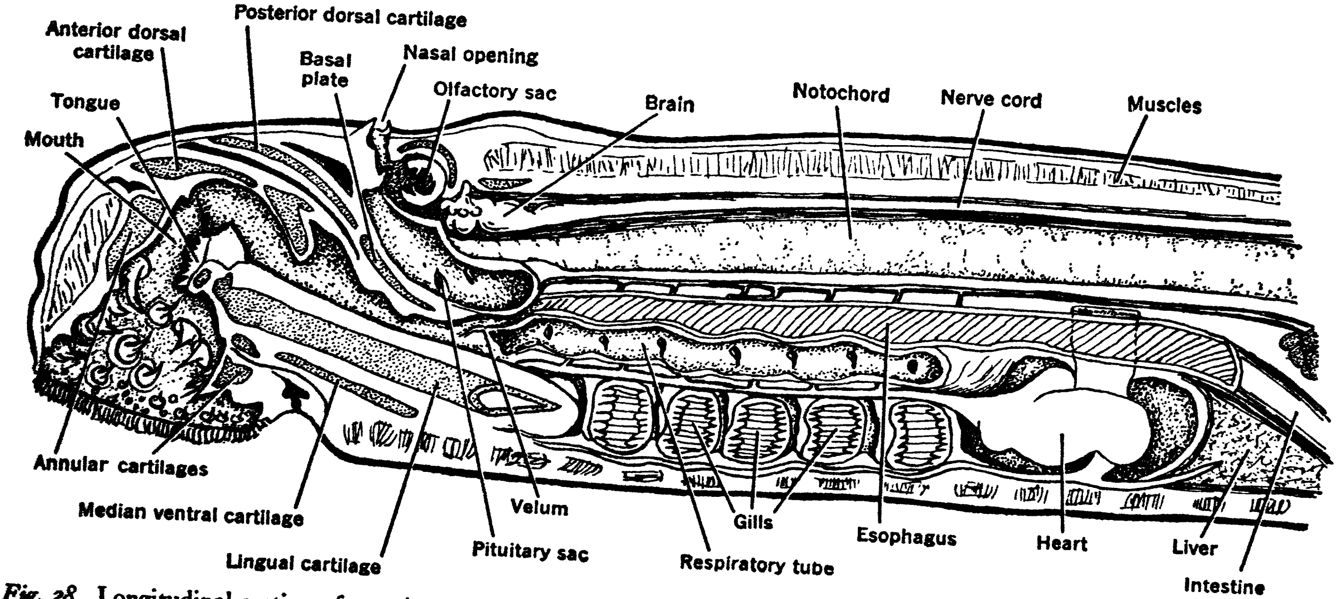


Fig. 28. Longitudinal section of anterior end of *Petromyzon*. (Adapted from Perrier Cepede Zoölogical Chart, courtesy of the Dennoyer-Geppert Company, Chicago.)

6. A row of mucous pores is present on each side of the body.
7. The brain is primitive and unmodified.
8. There is but one semicircular canal in the inner ear but it has two ampullae instead of the usual one.
9. The kidney tubules retain their primitive metamerism.

Petromyzontia. The lampreys are found in both salt and fresh water, the fresh-water forms usually being smaller than the marine species. They destroy numerous fishes, usually attacking them just below the pectoral fin. When the body wall is pierced by the action of the rasping tongue, the blood is sucked from the body of the host. During this procedure, passage of water through the mouth cannot take place, and respiration is carried on by currents of water flowing into and out of the gill slits. The common representative of this group is *Petromyzon marinus*, the sea lamprey.

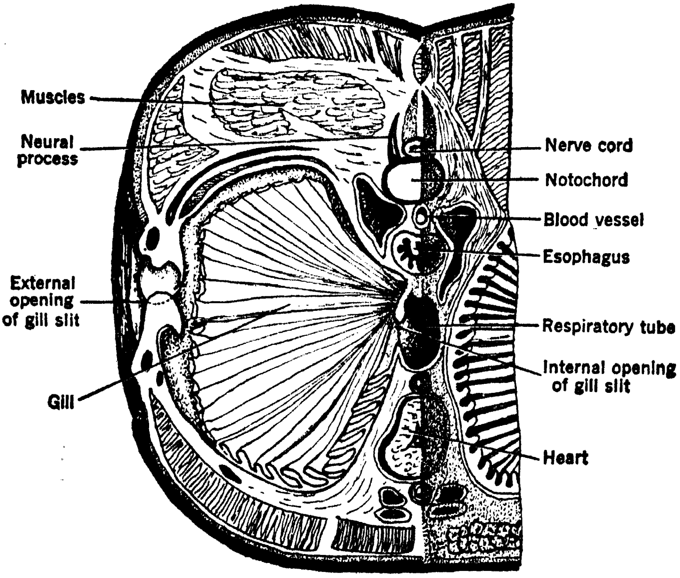


Fig. 29. Cross section of *Petromyzon* through the pharynx, with the right half cut at an angle. (Adapted from Perrier Cepede Zoölogical Chart, courtesy of the Dennoyer-Geppert Company, Chicago.)

Characteristics of the suborder include the following:

1. The mouth is surrounded by a cuplike oral funnel which is provided with horny "teeth."

2. The pituitary sac ends blindly below the brain (Fig. 28).
3. Neural processes are not confined to the tail region (Fig. 29).
4. A well-developed branchial basket is present.
5. A rudimentary spiral valve is found in the intestine.
6. The brain, with a distinct cerebrum and cerebellum, is more complex than that of the myxinoids.
7. There are two semicircular canals in the inner ear.
8. The gill slits are seven in number.
9. The kidney tubules are not segmentally arranged.

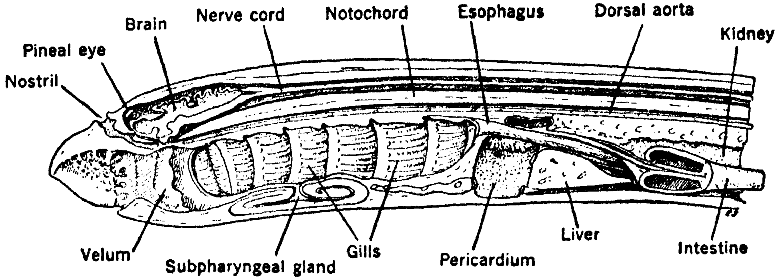


Fig. 30. Enlarged sagittal section of the *Ammocoete larva* of *Petromyzon.* (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

The position of the cyclostomes in relation to the other vertebrates presents an interesting problem. Although the cyclostomes resemble fishes in many ways, it has been found difficult, if not impossible, to establish definite relationships between the two groups. According to the views of many students of phylogeny, the ancestry of the cyclostomes can probably be traced back to some form resembling *Amphioxus*, from which they branched off prior to the origin of the fishes. According to this view, all other vertebrate classes have developed along a line of evolution entirely different from that which the cyclostomes less successfully followed.

A close relation to *Amphioxus* is at least suggested by the interesting development of the lampreys. The larval lamprey, *Ammocoetes* (Fig. 30), resembles *Amphioxus* in many ways and is of much interest because of its many primitive features. It has a hoodlike funnel at the anterior end and, within the pharynx, are several ciliated grooves and ridges somewhat resembling those of *Amphioxus*. A complicated structure located ventral to the pharynx and known as the subpharyngeal gland was long considered to be homologous to the endostyle of *Amphioxus*. Such homology is now considered rather doubtful as it has been shown that this structure has nothing to do with feeding.

After a long larval period of from two to five years, a rapid and striking metamorphosis takes place. This involves many changes, particularly in the pharyngeal region. During metamorphosis portions of the subpharyngeal gland give rise to the thyroid gland of the adult. For this reason it was formerly believed that the thyroid gland of the vertebrates was homologous to the endostyle of *Amphioxus*. This belief seems now to be untenable if, as suggested above, the subpharyngeal gland is not the homologue of the endostyle. Other changes in the pharynx include the pinching off of a dorsal tubular portion which becomes the esophagus. The remainder of the pharynx is the respiratory tube which communicates with the branchial pouches on either side and ends blindly anterior to the pericardial cavity.

Chondrichthyes Osteichthyes [1]

General characteristics. Like the cyclostomes, the members of these two classes are all aquatic, with those modifications of structure which make possible life in a liquid medium. The body of a typical fish (Fig. 31) is elongated, laterally flattened, and gradually tapering toward both ends. The skin characteristically contains bony or horny plates, the scales. The chief organ of locomotion is the caudal fin, which surrounds the tail. Other median fins, supported by bony or cartilaginous rays, are present along the dorsal margin, and in some forms similar structures occur ventrally posterior to the anus. Paired fins, the anterior pectorals and the posterior pelvics, are attached to bony or cartilaginous girdles, and are used as steering and balancing organs. Respiration is by means of gills, the membranes of which are bathed by water entering the mouth and leaving by the gill slits. The latter open directly to the external surface in some forms, while in others they are covered by a membranous or bony fold of the skin, the operculum.

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[1] These two classes have often been treated as subdivisions of the class Pisces which included all fishes. The modern tendency is to separate the cartilaginous from the bony fishes, and to give to each group the rank of a class. Although following this plan the author still finds it more convenient to describe them together as far as their general characteristics are concerned.

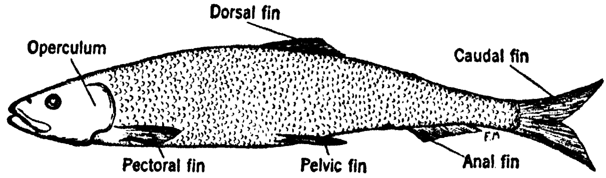


Fig. 31. A typical fish, the herring, *Clupea harengus*, showing body form and position of fins.

The circulatory system is of the type characteristic of those vertebrates having a branchial (gill) method of respiration. The blood is pumped anteriorly in a ventral aorta by the heart, which consists of two chambers, one auricle and one ventricle. From the ventral aorta the blood passes through the capillaries of the gills, where aeration takes place, and then to the dorsal aorta, by way of which it is distributed to various parts of the body.

The alimentary canal is short, consisting of a large pharynx, a short esophagus, a relatively simple stomach, and a short intestine. The digestive and absorptive surface is increased by such structures as the spiral valve or various types of caeca.

The excretory system consists of paired kidneys of the mesonephric type with ducts leading to an external opening or to a cloaca.

The sexes are separate, the reproductive organs consisting of testes and ovaries, with genital ducts which are more or less closely related to the excretory ducts. A majority of fishes are oviparous (egg-laying), while some are viviparous (giving birth to living young).

The skeleton is well developed, consisting of cartilaginous or bony elements, which may be grouped into axial and appendicular divisions. Portions of the notochord remain in some of the primitive orders. The mouth is closed by a hinged lower jaw.

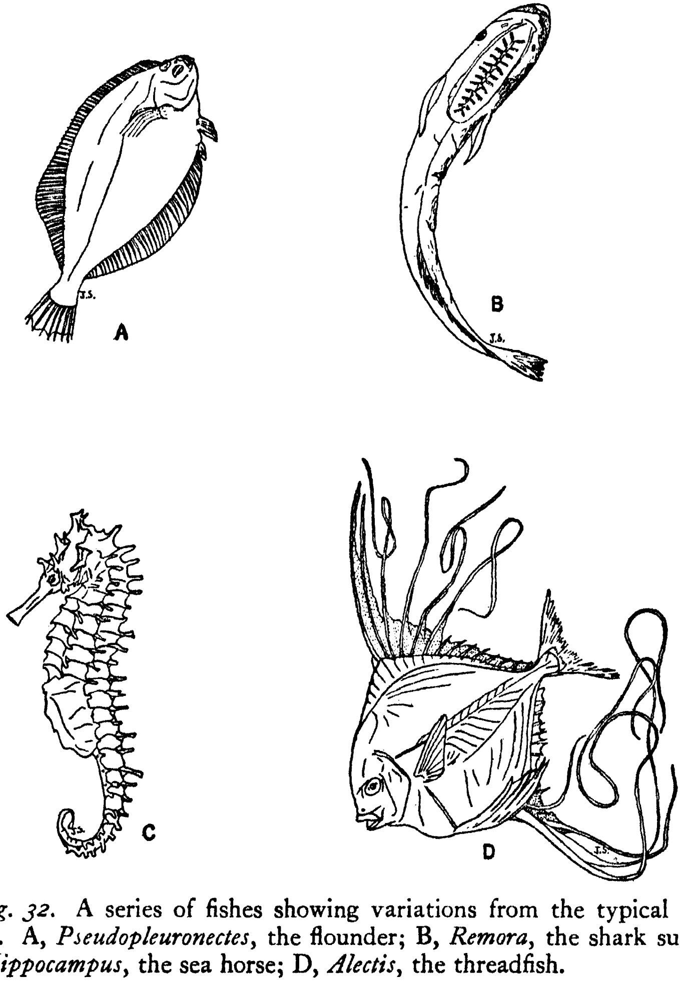
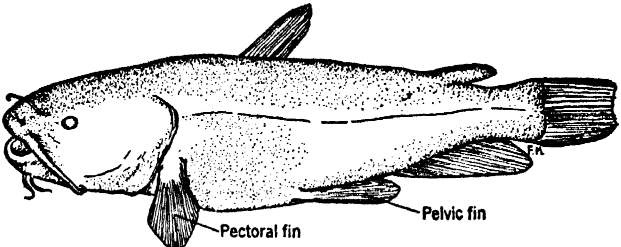


Fig. 32. A series of fishes showing variations from the typical body form. A, *Pseudopleuronectes*, the flounder; B, *Remora*, the shark sucker; C, *Hippocampus*, the sea horse; D, *Alectis*, the threadfish.

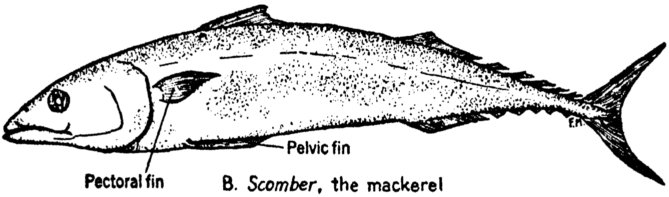
A number of special sense organs are arranged in a linear series on either side of the body in what is known as the lateral line. These are probably concerned with the perception of vibrations in a liquid medium.

Taste buds are more numerous than in the other vertebrate classes, being quite widely distributed in the skin of the head region.

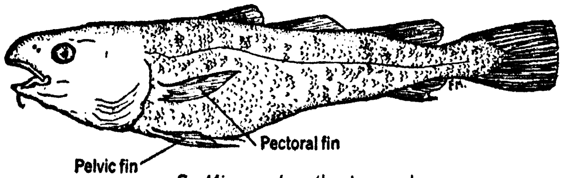
The brain is small and without flexures or bendings. There are ten pairs of cranial nerves. Of the special sense organs, the eyes are best developed, being much like those of the higher vertebrates except that they have spherical lenses adapted for short-range vision in water. The olfactory organs are paired and, in the typical members of the two classes, end blindly instead of communicating with the pharynx, as they do in the higher vertebrate classes. The auditory apparatus is not visible externally. It consists of three well-developed semicircular canals, and other internal structures which are concerned chiefly with equilibration,



A. *Ameiurus*, the cat fish



B. *Scomber*, the mackerel



C. *Microgadus*, the tom cod

Fig. 33. A series of bony fishes, showing the anterior migration of the pelvic fins. In C the pelvic fins are slightly anterior to the pectorals.

although recent investigation indicates that certain types of sound are heard.

CHARACTERISTICS OF CHONDRICHTHYES. This class contains those fishes which have a cartilaginous skeleton. They differ from the cyclostomes in having jaws, paired fins, and paired nostrils. The scales are of the placoid type. They are without lungs or air bladders. The mouth is ventral. In the male the pelvic fin has a clasper.

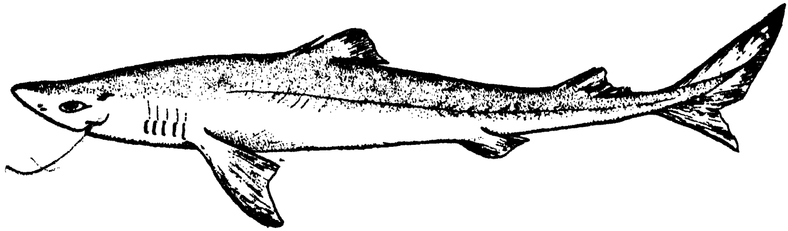


Fig. 34. A typical elasmobranch, *Squalus acanthias*, the spiny dogfish.

CLASSIFICATION. The living representatives of this class are divided into two orders: Elasmobranchii and Holocephali.

Elasmobranchii. The most common representatives of this order are the sharks (Fig. 34), the skates (Fig. 37C), and the rays. Much variation in body form is illustrated, ranging all the way from the fusiform generalized type of the dogfish to the dorso-ventrally flattened bottom-living skate or ray. The mouth is ventral rather than terminal (Fig. 35). The gill slits open directly to the outside surface and are more numerous than in the other fishes. A rudimentary gill slit, the spiracle, is present. The scales are of the placoid type, while the skeleton is composed entirely of cartilage. Fertilization is internal and in many species the young are born alive. The tail is of the heterocercal type (Fig. 36), with the vertebral column extending into the dorsal lobe, thereby

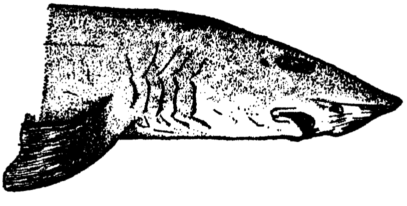


Fig. 35. Head of an elasmobranch showing ventral mouth and open gill slits.

forming a structure which is asymmetrical both internally and externally. The elasmobranchs also differ from most other fishes in the presence of a spiral valve in the intestine (Fig. 255). A cloaca is present and the jaw suspension is hyostylic (Fig. 217).

Holocephali. This order contains but three genera of deep-sea forms, of which *Chimaera* (Fig. 38) is perhaps the best known. They differ from the elasmobranchs in the method of suspension of the jaws (holostylic), in the modification of the teeth into crushing plates, in the development of a rudimentary operculum, and in the absence of a cloaca and spiracle.

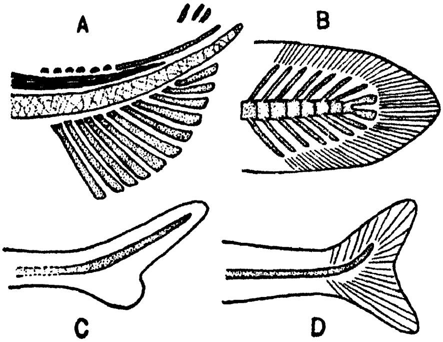


Fig. 36. Diagrams of types of tails in fishes. A and C, heterocercal; B, diphycercal; D, homocercal. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

Characteristics of Osteichthyes. This class contains a large majority of the more common fishes. Their most important characteristics are just the opposite of those which characterize the Chondrichthyes. The skeleton is partially or wholly bony and consists of many separate elements. Some of these result from the ossification of the primitive cartilaginous skeleton; while others, particularly those related to the upper and lower jaws, the operculum, and the pectoral girdle, are investing bones, formed in the integument. The scales may be of the ganoid, cycloid, or ctenoid type, but are never placoid. The gill slits are covered by an operculum.

An air bladder is present but claspers are not.

Classification. The class is divided into subclasses, orders, and suborders as follows:

Subclass — Choanichthyes
  Order — Crossopterygii
  Order — Dipnoi

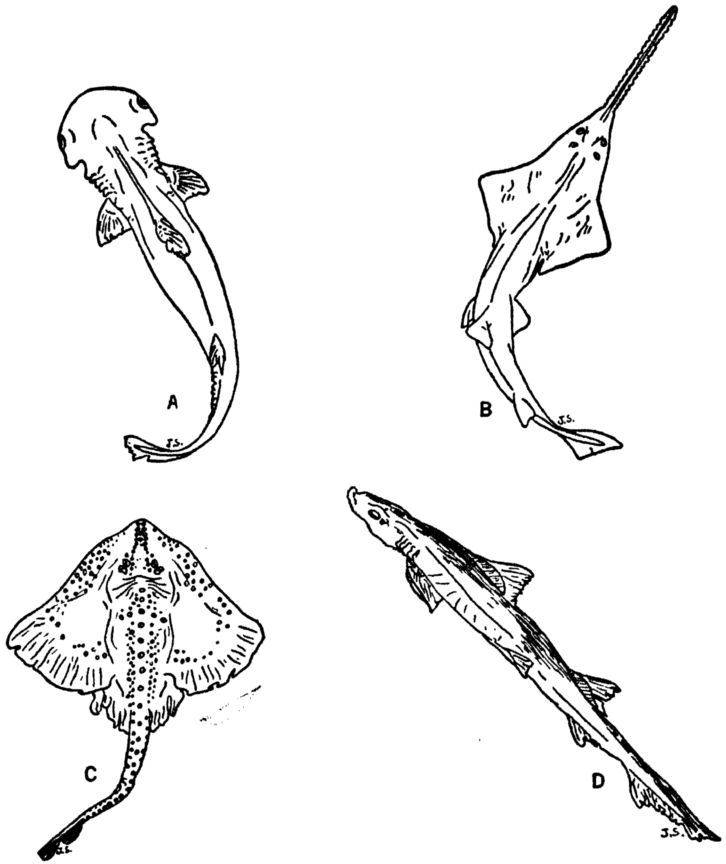


Fig. 37. A series of elasmobranch fishes, showing variations in body form. A, *Sphyrna tiburo*, the bonnet-head shark; B, *Pristis pectinatus*, the sawfish; C, *Raii erinacea*, the common skate; D, *Mustelus canis*, the smooth dogfish.

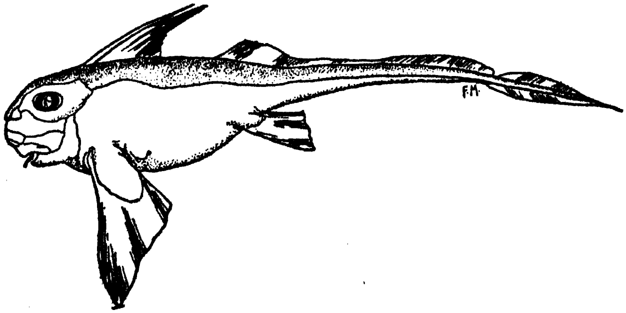


Fig. 38. A holocephalan, *Chimaera monstrosa.*

- Subclass — Actinopterygii (Teleostomi)
  - Order — Chondrostei
    - Suborder — Polypterini
    - Suborder — Acipenseroidea
  - Order — Holostei
    - Suborder — Lepidosteoidei
    - Suborder — Amioidea
  - Order — Teleostei

Subclass Choanichthyes

The members of this subclass, as the name implies, have nostrils which open into the mouth cavity instead of ending blindly as is the case in most aquatic vertebrates. The paired fins are supported by a basal lobe. The air bladder functions as a lung. The scales are large and are rounded or rhomboidal in shape.

Order *Crossopterygii*

This group have paired fins with rounded basal lobes. Because of this they have long been known as lobe-finned fishes. The attachment to the pectoral girdle is by means of a single bone. The jaw suspension is hyostylic. They have a spiracle.

This order is of particular interest as the probable ancestors of land-living vertebrates. Long considered an extinct group, a living representative was caught off the coast of Africa in 1939. This living fossil has been called *Latimeria.*

Order *Dipnoi*

The lungfishes are represented by three living genera: *Epiceratodus* of Australia, *Lepidosiren* of South America, and *Protopterus* (Fig. 39) of Africa. Their paired fins have elongated jointed axes which give rise to side branches. A spiracle is absent and a spiral valve is present. The jaw attachment is autostylic. The tail is diphycercal, that is, having both internal and external symmetry.

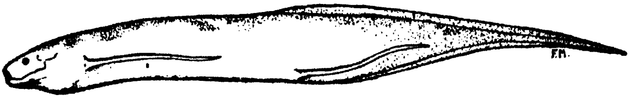


Fig. 39. The African lungfish, *Protopterus.*

Subclass Actinopterygii (Teleostomi)

In this large subclass the paired fins do not have a basal lobe and the fin rays are attached directly to the girdles (with the few exceptions mentioned below). They are referred to as ray-finned fishes. The jaw suspension is hyostylic. The nasal cavities do not communicate with the mouth cavity. There are separate anal and urogenital openings.

Order *Chondrostei*

This order contains few living representatives. The skeleton is largely cartilaginous. A spiral valve is present and often a spiracle. The scales are of the ganoid type. They are often referred to as cartilaginous ganoids.

Suborder *Polypterini*

The two living members of this suborder, *Polypterus* (Fig. 40) and *Calamoichthyes*, differ from typical teleostomes in having pectoral fins with basal lobes. For this reason they were formerly classed as crossopterygians. The paired lungs open into the ventral floor of the esophagus.

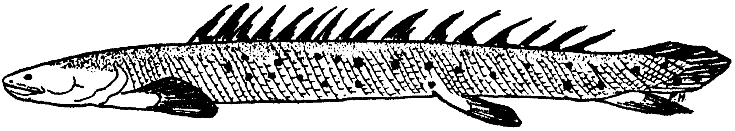


Fig. 40. A chondrostean, *Polypterus bichir.*

Suborder *Acipenseroidea*

This suborder contains two types, the sturgeons, *Acipenser* and *Scaphyrhynchus* (Fig. 41); and the paddlefishes of which *Polyodon* (Fig. 41) is the typical genus. They have a long snout or rostrum with a ventral mouth. The tail is heterocercal. The notochord is persistent and the vertebrae are incomplete. The lung opens dorsally.

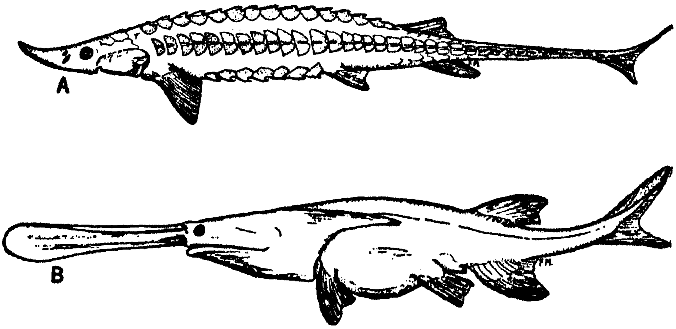


Fig. 41. Two chondrosteans. A, *Schaphirhynchus platyrhynchus*, a sturgeon; B, *Polyodon spathula*, the paddlefish.

In the sturgeons, the broad winglike bony scales are arranged in longitudinal rows, separated by wide areas bearing small scales. The ventral surface of the head contains small sensory structures, the barbels.

The paddlefishes have long spatulate rostra. They are common in the Mississippi river and its tributaries. The skin has very few scales. They are of the ganoid type and are confined to a small region in the tail.

Order *Holostei*

The members of this order are often referred to as bony ganoids. The skeleton is more fully ossified than in the preceding order, but ganoid scales are not always present. There is no spiracle. A single dorsal air bladder opens dorsally.

Suborder *Lepidosteoidei*

Lepidosteus (Fig. 42), the fresh-water garpike of North America is the only genus. They have a long cylindrical body with a long narrow snout. The body is covered with a continuous armor of heavy tilelike ganoid scales. The tail is modified heterocercal. The air bladder is used as a lung.

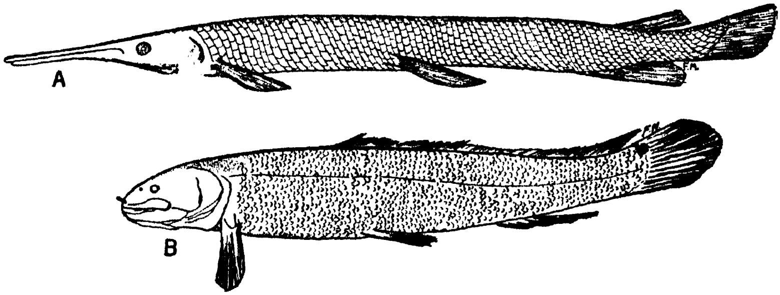


Fig. 42. Two holosteans. A, *Lepidosteus tristaechus*, the alligator gar; B, *Amia calva*, the bowfin.

Suborder *Amioidea*

Amia calva (Fig. 42), the "bowfin," the only living species, is found in the Mississippi and St. Lawrence rivers and in their tributaries. The name "bowfin" is derived from the fact that there is a continuous dorsal fin. The scales are large and of the cycloid type. The tail is modified heterocercal. The air bladder is used in respiration.

Order *Teleostei*. The bony fishes.

This order contains a great majority of the best-known fishes, such as the trout, cod, and salmon. Such a wide variation of structure is seen in the great groups of teleost fishes that it is difficult to list distinctive features. It can be said, however, that the skeleton is well ossified, the scales are cycloid or ctenoid, and the tail is usually homocercal. A tail of this type is apparently symmetrical as far as the external appearance is concerned, but is asymmetrical internally. There is no spiracle. The single air bladder is dorsal and often ductless. There is no spiral valve.

Amphibia

Biological importance of the class. Although a relatively small group of no great economic importance at the present time, the amphibia are of great interest to the biologist because of the unique position they occupy in nature. The two classes previously considered are aquatic, while those remaining for consideration are predominantly terrestrial. The amphibia, as the name implies, are very much at home in either habitat. Although a few species are permanently aquatic, while others are mainly terrestrial, nearly all members of the class spend their larval life in the water. Because of this necessity of returning to the water for breeding purposes, the group is not widely distributed, being mainly confined to swamps or marshes, or to a rather restricted area adjoining some body of water.

In the lifetime of many members of this group there is illustrated for us the modifications involved in a great evolutionary step; namely, the change from an aquatic to a land environment, or more essentially, from a water medium to one of air. If we study the development of one of the higher amphibia from its fishlike larval (Fig. 43) stage into a moderately successful land-living animal, we see a brief and simplified summary of the far-reaching changes the higher vertebrates must have gone through in ages past, while evolving from their aquatic ancestors.

The change from a liquid to a gaseous medium involves a profound modification of those structures concerned with three important functions of living organisms; namely, locomotion, respiration, and reproduction. The problems of locomotion upon land are obviously very different from those arising in water. The system of fins so successfully used for this purpose by the fishes could not function upon land in the less buoyant medium of air. To function properly upon land any locomotor apparatus must do two things: support the weight of the body and serve to move it from one place to another. In the amphibian for the first time we see the development of such an apparatus in the form of the two paired appendages, the fore and hind limbs. Consisting of a jointed series of long bones attached to other skeletal parts, known as girdles, and moved by means of numerous muscles,

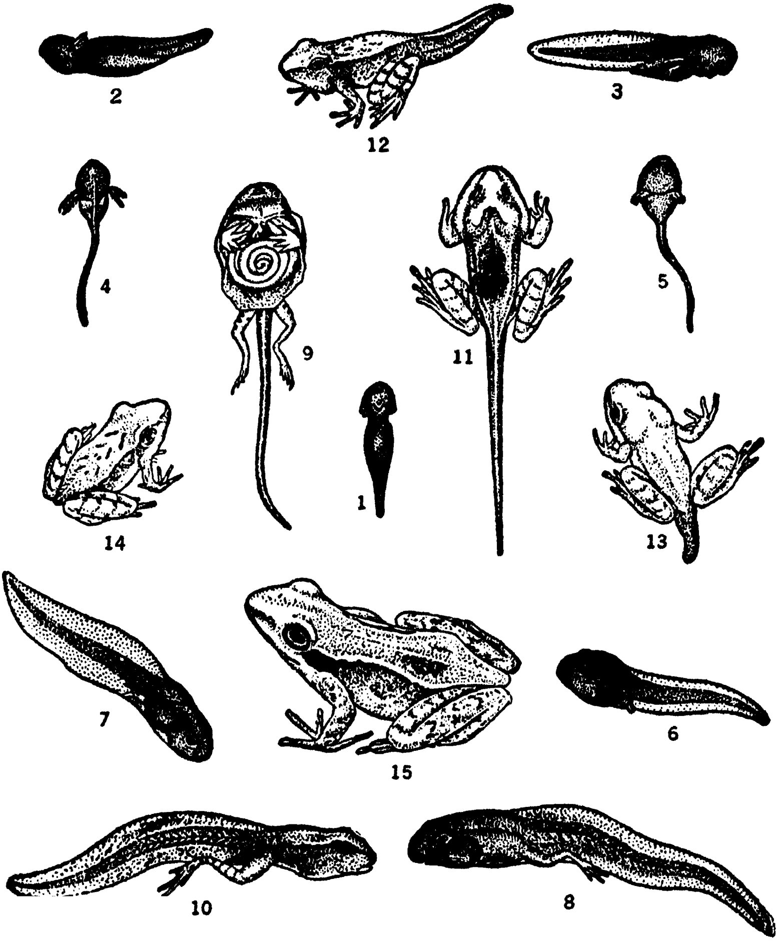


Fig. 43. Larval development and metamorphosis of the frog. 1, tadpole just hatched, dorsal aspect. 2, 3, older tadpoles, side view. 4, 5, later stages, dorsal views showing external gills and development of operculum. 6, 7, older stages showing hind leg. 8 and 10, lateral view of two later stages showing development of hind legs. 9, dissection of tadpole to show internal gills, spiral intestine, and anterior legs developed within operculum. 11, advanced tadpole just before metamorphosis. 12, 13, 14, stages in metamorphosis, showing, gradual resorption of tail. 15, juvenile frog after metamorphosis. (From Hegner, *College Zoölogy*, after Leuckart-Nitsche wall chart, by permission of The Macmillan Company, publishers.)

the limbs act like levers which propel the body forward or backward. As would be expected in this early stage of development, these appendages are not very efficient as organs of locomotion. Because of the manner in which the long bones are attached to the girdles, the limbs project laterally from the sides of the body rather than ventrally beneath it. As a result, they are hardly capable of supporting the weight of the body above the ground, to say nothing of moving it along the surface. The great importance of the appendages of the amphibian, then, lies in the significant changes from the preceding type rather than in any great degree of efficiency which they possess.

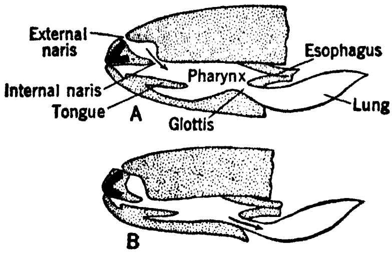


Fig. 44. Diagrams illustrating respiratory movements of the frog. A. The floor of mouth is depressed and the nares are open and air is drawn into the pharynx. B. The floor of the mouth is raised and the nares are closed, forcing the air from the pharynx into the lungs. (Redrawn from Holmes, *Biology of the Frog*, after Parker and Parker.)

In the matter of respiration also, the change involved in coming from water into air is equally revolutionary. As we have seen, the chief organs of respiration of the fishes and cyclostomes are the gills. These structures consist of thin membranes through which the needed oxygen passes from the water on one side into the blood stream on the other. Since any respiratory membrane must be kept moist in order to function, such structures as gills would not be satisfactory in terrestrial forms, as the membranes would dry up on exposure to the air. In land-living animals, therefore, an entirely different respiratory apparatus is needed, and this need has been met in the development of the lungs, which eventually replace the gills as organs of respiration (Fig. 44). A lung is a membranous sac located within the body for protection against desiccation, provided with a regulated inlet and outlet for the respiratory medium (air) and plentifully supplied with blood vessels. Because of the environment in which the amphibians live during the larval stage, they are provided with functional gills during this period. Some forms, such as *Necturus*, which is a permanently aquatic type and possibly a permanent larva, have both gills and lungs present and functional at the same time. The lungs in such a case are primitive and simple sacs which probably play a minor role in respiration. In a majority of the amphibians however, the gills are replaced in adult life by functional lungs. The skin, also, should be mentioned as an important organ of respiration in this group of vertebrates. Provided with mucous glands which keep it moist, and having a plentiful blood supply, it has all the necessary attributes of a respiratory membrane.

Important modifications in the circulatory system have paralleled the change from the branchial (gill) to the pulmonary (lung) type of respiration. The heart consists of three chambers: two auricles and one ventricle. Instead of containing venous blood only, as in the fishes, there is at least a partial separation of arterial from venous blood within the heart. After passing through the pulmonary circulation (to the lungs and skin), the blood is returned to the heart before being distributed throughout the body in the systemic circulation.

Although somewhat successful in the development of locomotor and respiratory structures adapted to their new environment, the amphibians were not so fortunate in respect to the third function previously mentioned, reproduction. Fertilization is typically external as in a majority of water-living forms, and, as embryonic membranes do not appear until a later date in vertebrate history, a liquid medium is essential, not only for fertilization but also for the subsequent development of the fertilized egg. Because of these facts the group has never become entirely independent of a water environment.

CHARACTERISTICS. With the exception of the general modifications of structure which have just been described and which are significant chiefly in the light of what is to follow, it is difficult to assign any very distinctive characteristics to the amphibians. It can be said, of course, that their larval life is spent in the water and that a majority of them become semiterrestrial forms after a more or less rapid metamorphosis (Fig. 43). The skull articulates with the atlas, or first cervical vertebra, by two occipital condyles, located on the exoccipital bones. There is external evidence of an auditory apparatus, in the form of the tympanic membrane, which communicates with the inner ear by means of a single bone, the columella. The appendages are of the four-footed (tetrapod) and five-fingered (pentadactyl) type. Claws are not present at the tips of the digits. The heart consists of two auricles and one ventricle. The skin is moist and smooth, there being no scales in a majority of the species.

The preceding characteristics serve to separate the amphibians from the fishes and cyclostomes, while they may be distinguished from the higher vertebrates by the following features. The kidneys are provided with persistent nephrostomes, or openings into the body cavity. Gills are present during the early stages of development. There are but ten cranial nerves.

Of the characteristics mentioned, perhaps the absence of scales and claws is the most useful, as it serves to distinguish them from such reptiles as the lizards, which some of the amphibians (salamanders) superficially resemble.

CLASSIFICATION. The living amphibians may be divided into three orders as follows:

1. Gymnophiona — Limbless forms
2. Caudata — Amphibians with tails in the adult
3. Salientia — Amphibians without tails in the adult

Gymnophiona (*Apoda*). These are limbless forms (Fig. 45) resembling the segmented worms in many respects. There are about fifty-five species, widely distributed throughout the tropics. They are burrowing animals, with rudimentary and practically functionless eyes. In this group internal fertilization is the practice. A protrusible tentacle between the nostril and the eye, and the presence of deeply set dermal or bony scales are other distinctive features. Some genera are oviparous, while others are viviparous. *Caecilia* is one of the best-known examples.

Caudata (*Urodela*). This order includes about one hundred species commonly known as newts, salamanders, or mud puppies (Fig. 46). Some of the urodeles, such as *Necturus maculosus*, the common American mud-puppy, and *Proteus*,

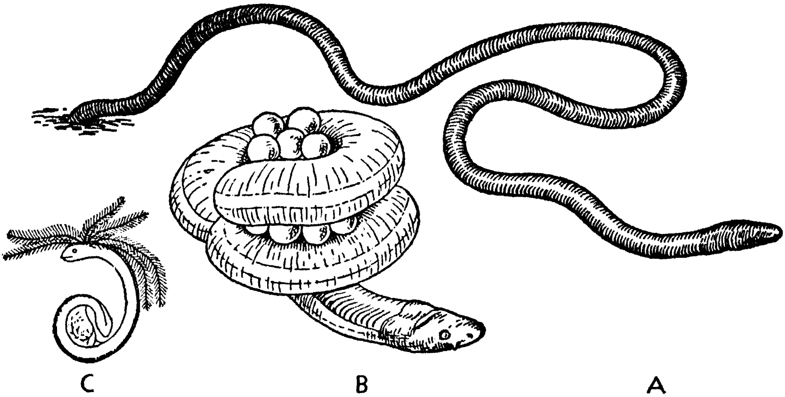


Fig. 45. Group of apoda. A, *Caecilia*, emerging from burrow; B, *Ichthyophis glutinosus* (nat. size), female guarding her eggs, coiled up in hole in the ground; C, a nearly ripe embryo, with cutaneous gills, tail-fin, and still a considerable amount of yolk. (From Newman, *The Phylum Chordata*, redrawn after P. and F. Sarasin, by permission of The Macmillan Company, publishers.)

the blind "Olm" of Germany, have three pairs of external gills throughout life. *Siren lacertina*, the "mud eel," also has three pairs of permanent external gills, but differs from the two forms just mentioned in having no hind limbs. Although these species were formerly considered primitive because of this retention of functional gills during adult life, it seems more likely that they are permanent larvae. This retention of larval structures in a sexually mature animal is known as paedogenesis.

The other urodeles, commonly known as salamanders or newts, are without gills in the adult, although gill clefts may remain. *Ambystoma tigrinum*, the tiger salamander, and *Triturus viridescens*, the crimson-spotted newt, are well-known examples of this group. *Cryptobranchus alleghaniensis*, the "hellbender," is one of the largest salamanders of this country, reaching a length of nearly two feet. In this form a single pair of gill slits remains in the adult. The eyes are small and without lids. An oriental genus, *Megalobatrachus*, is the largest living amphibian, sometimes reaching a length of over five feet. These two genera are considered to be examples of incomplete metamorphosis. *Amphiuma means* is an eel-shaped salamander, having very small limbs with a reduced number of digits. This animal has become quite well known for having the largest red blood corpuscles of any animal. Other cells of the body are also relatively large.

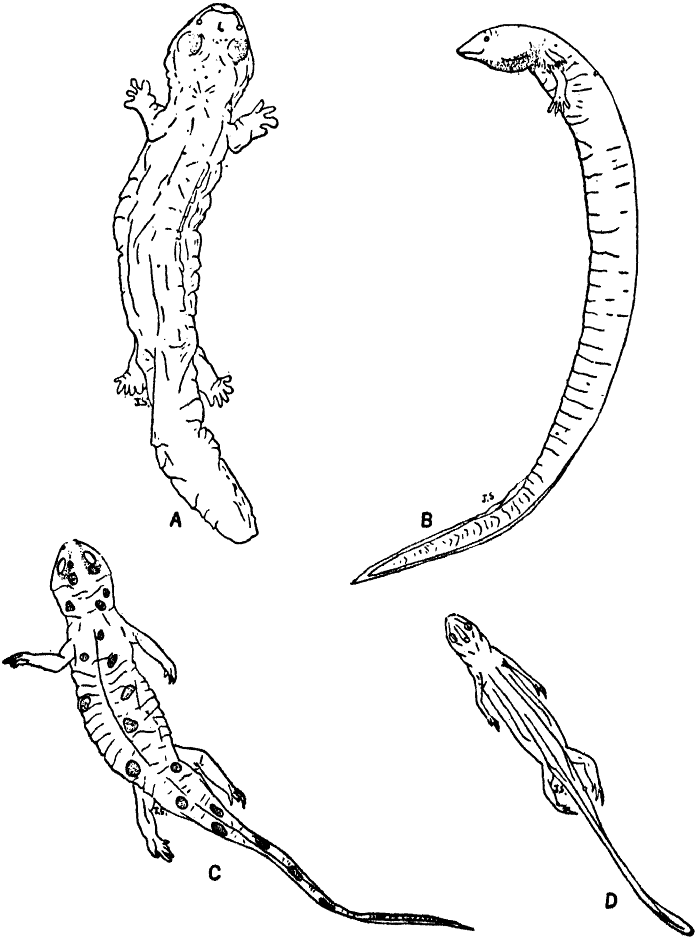


Fig. 46. A series of amphibians. A, *Cryptobranchus*, the hellbender; B, *Siren*, the mud eel; C, *Ambystoma*, a spotted salamander; D, *Triturus*, a common newt.

One family of urodeles, the Plethodontidae, is of particular interest because of the absence, in the adult, of both gills and lungs. In the members of this family, the skin and the walls of the pharynx and esophagus are used as respiratory membranes. Examples of this group are *Plethodon* and *Desmognathus*.

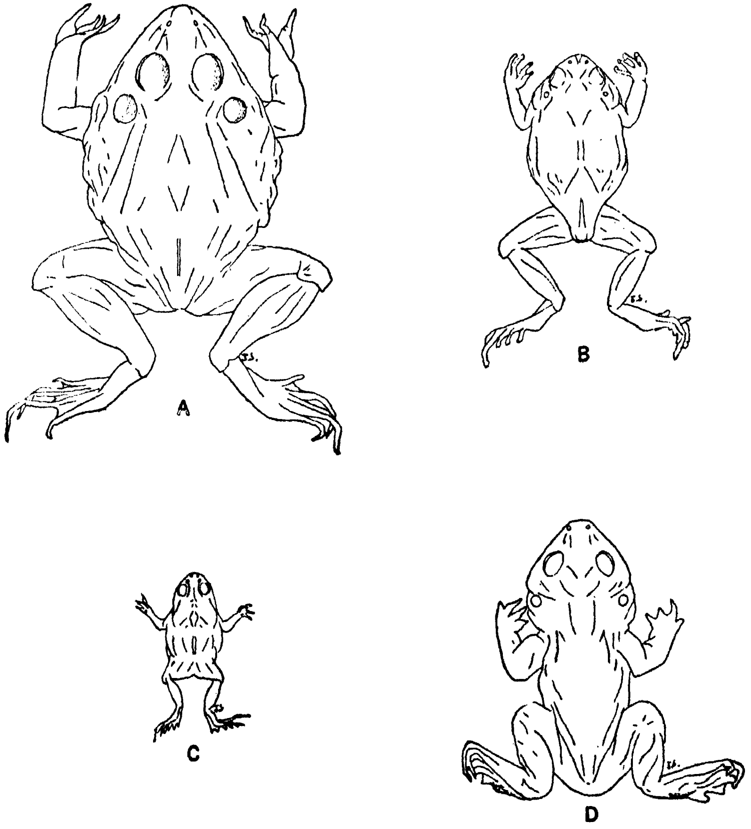


Fig. 47. A series of anurans. A, *Rana aesopus*, the gopher frog; B, *Hyla versicola*, the common tree frog; C, *Bufo quericus*, the oak toad; D, *Scaphiopus holbrookii*, the spadefoot toad.

Salientia (Anura). This order, including the frogs and toads (Fig. 47), contains about seventeen hundred species. They are characterized by short, tailless bodies and long hind legs. In this group are found some of the most highly specialized examples of living amphibians. In this order are found for the first time such structures as lacrymal glands, movable eyelids, and sound-producing organs. Adaptations for terrestrial, arboreal, aquatic, or fossorial life are illustrated. The common bullfrog of laboratory fame, *Rana*

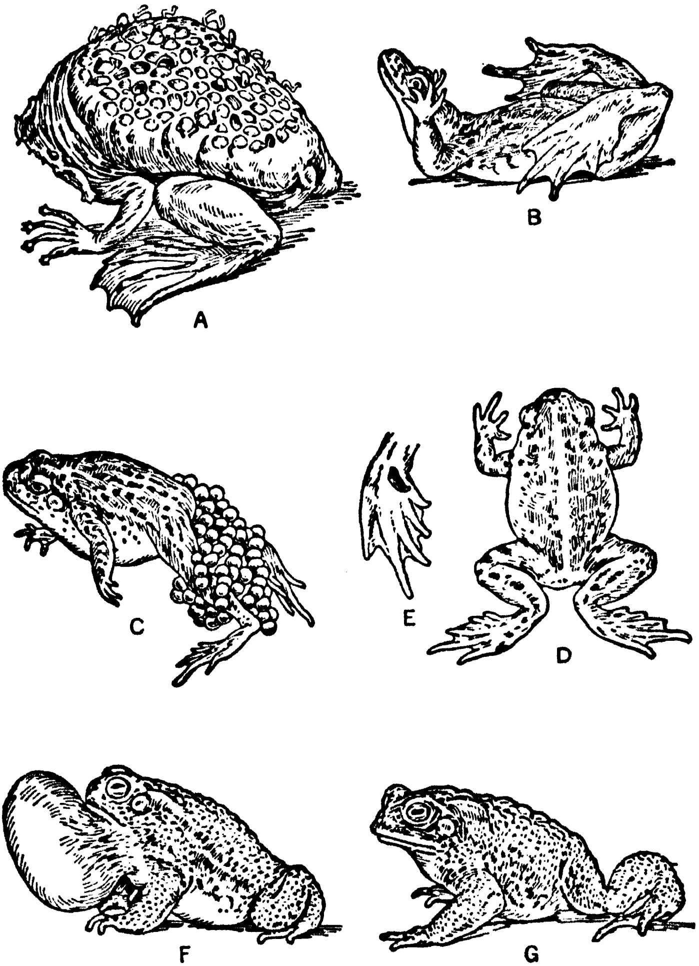


Fig. 48. Frogs and toads (anura). A, Surinam toad, *Pipa americana;* B, fire-bellied toad, *Bombinator igneus;* C, midwife toad, *Alytes obstetricans;* D, spadefoot toad, *Pelobates cultripes;* E, foot of *Pelobates* showing tarsal spur; F, common toad, *Bufo lentiginosus s. americanus*, with vocal sac inflated; G, same stalking its prey. (From Newman, *The Phylum Chordata.* A and C, redrawn after Lydekker; B, D, and E, redrawn after Gadow; F and G, redrawn after Dickerson. By permission of The Macmillan Company, publishers.)

catesbiana, is an aquatic form, while *Rana pipiens*, the "leopard frog," is largely terrestrial. Of the common toads of North America, *Bufo americanus* is perhaps the most typical. Feeding on worms and insects they are a valuable aid to the farmer in the control of pests. The genus *Hyla* is the most generalized of the so-called tree toads, which are provided with adhesive pads on the digits. *Hyla versicola* (Fig. 47B) is the common tree frog of the United States. *Acris gryllus*, the "cricket frog" of eastern United States, is one of our smallest frogs.

Several members of this order are of special interest because of their breeding habits. In *Pipa pipa*, the "Surinam toad" (Fig. 48), the eggs develop in pockets in the skin of the dorsal surface of the female. In *Alytes obstetricans*, of France and Switzerland, the male cares for the eggs which are attached in bunches to the hind legs. He keeps them moistened with dew until nearly ready to hatch, and then returns to the water with them. The female of *Nototrema marsupium* has a brood pouch in the back, formed by a fold of skin, in which the young are carried until nearly ready for metamorphosis.

Reptilia

This class of vertebrates, as far as living members are concerned, includes *Sphenodon*, the crocodilians, turtles, lizards, and snakes (Fig. 49). Although in times past a very large and important group, as an abundance of fossils indicates, only these five types have been able to survive to the present day. To the casual observer it is apparent that the forms here included differ widely from one another. Crocodiles and turtles at first sight appear to have few characteristics in common; and when one turns to the snakes, similarities of structure are even less apparent.

General characteristics. The most important and distinctive features of the reptiles are those modifications of structure which show an advance over the amphibian type and which have enabled the reptiles to become entirely independent of an aquatic environment. Although it is true that many reptiles today show secondary adaptations for an aquatic habit of life, as a group they are independent of such a medium from the very beginning of their development.

Among the various modifications which have made the reptiles the first definitely successful terrestrial vertebrates,

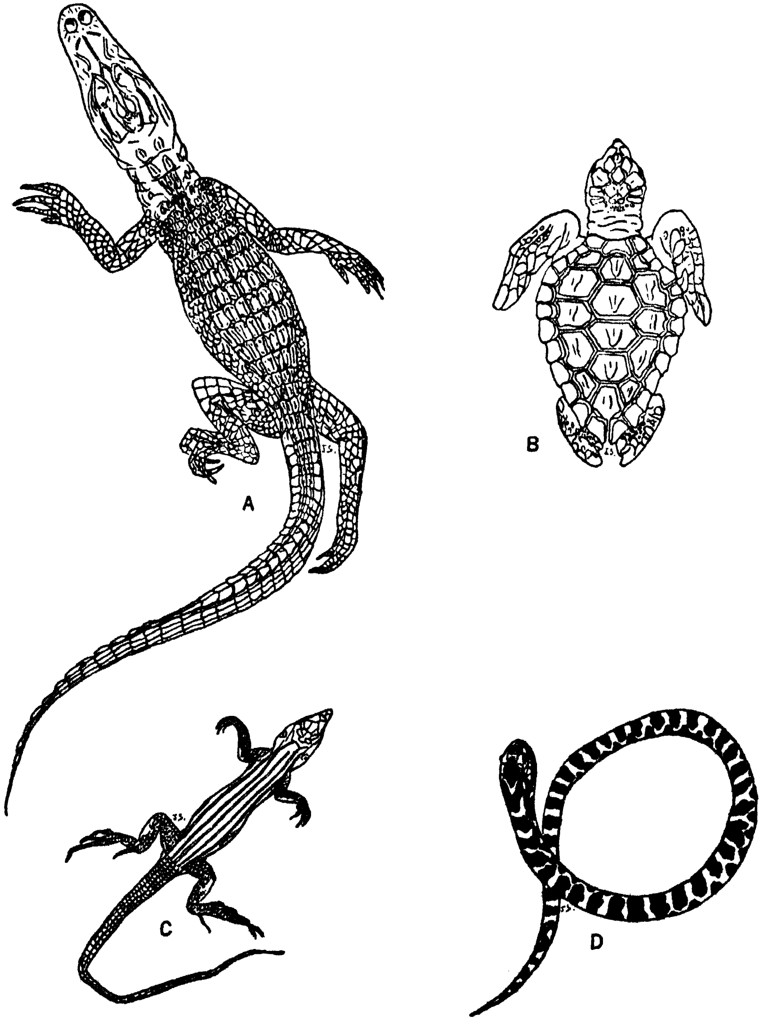


Fig. 49. A series of reptiles representing the four major groups of living reptiles. A, *Alligator mississippiensis*, order Crocodilia; B, *Thallasochelys caretta*, order Chelonia; C, *Cnemidophorus sexlineatus*, order Squamata, suborder Sauria; D, *Lampropeltis triangulum triangulum* (young), order Squamata, suborder Ophidia.

the following are the most important: the presence of a scaly covering which aids in preventing loss of moisture from the skin; the development of a more efficient respiratory mechanism; and the acquisition of embryonic membranes, the amnion and allantois, which have made possible development of the embryo out of a water habitat.

It was previously stated that the skin of the typical amphibian is smooth and moist because of the presence of mucous glands. In the reptiles the skin is covered with horny scales which prevent excessive loss of moisture with resulting desiccation. As would be expected, the reptilian skin is not a satisfactory respiratory membrane. In this group the lungs are the only respiratory organs and are much more efficient structures than in the amphibians. Functional gills are entirely absent, even in the early embryonic stages of development.

The embryonic membranes (Fig. 50) which first appear in the reptile are structures adopted by all land vertebrates for development of the embryo outside of a water habitat. The amnion is a fluid-filled sac surrounding the embryo and developing from lateral folds of extraembryonic tissue comprising the outermost layer of ectoderm and mesoderm. Suspended in the watery fluid within this sac, the growing embryo is protected against desiccation as well as from mechanical injuries of all kinds. The amnion thus gives to the embryo of terrestrial forms an individual liquid medium with all the advantages of the natural environment in which all the preceding types undergo development. The other embryonic membrane, the allantois, takes the place of gills as the embryonic respiratory device. Beginning as a finger-like diverticulum from the posterior part of the primitive alimentary canal, it grows out between the amnion and the egg membrane, as a large and highly vascular sac consisting of endoderm and the inner layer of mesoderm. It increases in extent until it eventually lines a greater part of the inner surface of the egg membrane. The respiratory exchange of gases between the outer air and the blood stream within takes place through this membrane and the porous coverings of the egg. These two membranes, amnion and allantois, have been of great importance to the reptiles in making them practically independent of a water environment for breeding

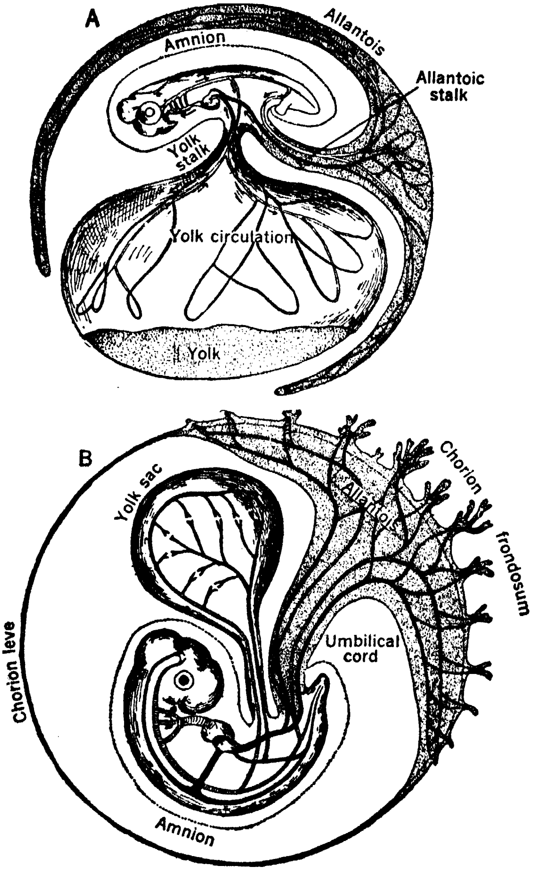


Fig. 50. Diagrams showing the relation of the embryonic membranes. A, a reptile or bird with functional yolk sac and respiratory allantois; B, mammal with functionless yolk sac and with the allantois converted into an umbilical cord and placenta. (Adapted from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

purposes, and have thus made possible a much more extensive distribution.

OTHER CHARACTERISTICS. Aside from the important modifications described above, a number of characteristics may be mentioned which distinguish the reptiles from other vertebrate classes. The following features will serve to separate them from the preceding groups:

1. One occipital condyle is present.
2. The lower jaw consists of many separate bones.
3. A true sternum is present.
4. The heart consists of two auricles and a partially divided ventricle.
5. Lateral line sense organs are absent.
6. The kidneys are of the metanephric type.
7. There are twelve cranial nerves.

The presence of two complete and functional aortic arches, the incomplete division of the ventricle, and such negative characteristics as the absence of feathers or hair and of a mechanism for warm-bloodedness distinguish them from the birds and mammals. There is always a typical cloaca present and fertilization is internal. A majority are oviparous. ✓

CLASSIFICATION. The modern reptiles (Fig. 49) may be divided into four distinct orders, as follows:

1. Rhynchocephalia — *Sphenodon* only
2. Chelonia — The turtles and tortoises
3. Crocodilia — Crocodiles and alligators
4. Squamata — Lizards and snakes
    Sauria (Lacertilia) — Lizards
    Ophidia — Snakes

Rhynchocephalia. This order contains but one living representative, *Sphenodon punctatum* (Fig. 51), the famous "living fossil" of New Zealand. This lizardlike animal possesses many primitive features, particularly in the bones of the skull and of the appendages. The presence of a third eye (parietal organ) in the median dorsal surface of the head is a distinctive feature.

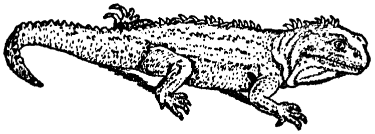


Fig. 51. Sphenodon punctatum. (From Newman, *The Phylum Chordata*, after Gadow, by permission of The Macmillan Company, publishers.)

Chelonia. The turtles (Fig. 52) are the most numerous of the reptiles in this country. The boxlike covering, consisting of a dorsal carapace and a ventral plastron made up of epidermal scales overlying a foundation of bony plates, is so distinctive of this group that additional characteristics are more or less superfluous. The presence of a horny beak at

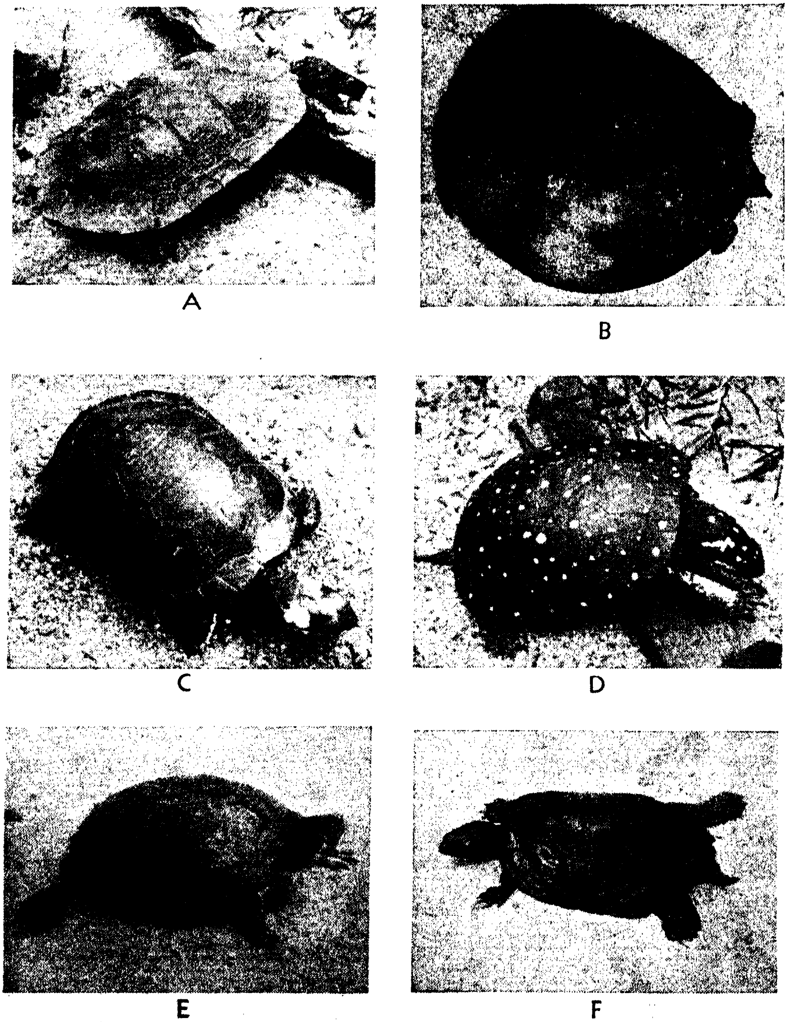


Fig. 52. A series of turtles. A, wood turtle, *Clemmys insculpta;* B, soft-shelled turtle, *Trionyx ferox;* C, Muhlenberg's turtle, *Clemmys muhlenbergii;* D, spotted turtle, *Clemmys guttata;* E, yellow terrapin, *Pseudemys sp.;* F, geographic terrapin, *Graptemys pseudographica.* (Courtesy N. Y. Zoölogical Society.)

the end of their toothless jaws is equally characteristic. They range from the purely marine types, such as *Eretmochelys* (Fig. 53), which come to land only for egg-laying purposes, through a variety of amphibious forms to the strictly terrestrial type, as illustrated by *Testudo* (Fig. 54), and other giant land tortoises inhabiting the oceanic islands.

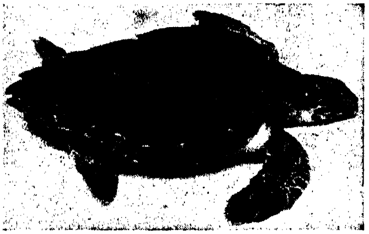


Fig. 53. Hawksbill turtle, *Eretmochelys imbricata.* (Courtesy N. Y. Zoölogical Society.)

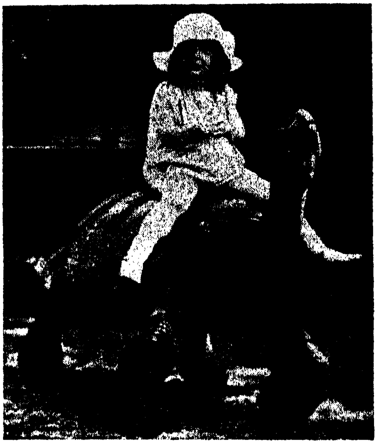


Fig. 54. Giant tortoise, *Testudo vicina*, from the Galapagos Islands. Weight, two hundred and seventy pounds. (Courtesy N. Y. Zoölogical Society.)

The use of the common terms, such as turtles, tortoises, and terrapins (Fig. 55), has become so careless as to cause more or less confusion to the average person. According to Ditmars, tortoises are the strictly terrestrial forms; turtles, semiaquatic and marine; and terrapins, the hard-shelled, fresh-water, and edible species.

The snapping turtle, *Chelydra serpentina*, is one of the most generalized forms. *Chrysemys picta*, the painted turtle, and *Terrapene carolina*, the box-turtle, are common species in the Southern and Eastern states (Fig. 56).

Fig. 55. Cumberland terrapin "slider," *Pseudemys elegans.* (Courtesy N. Y. Zoölogical Society.)

Crocodilia. The members of this order differ from the turtles in having a more generalized and better proportioned body form. The tail is long, the limbs are well developed, and no region of the body is emphasized as compared with the rest. The lungs are large and more efficient as organs of respiration than in other reptiles. The circulatory system, also, is more highly developed than in the other members of the class. The heart is large and represents an advance over that of other reptiles in that a longitudinal septum divides the ventricle into a right and left chamber. This results in a practically complete separation of arterial from venous blood, as in the birds and mammals. The brain is well developed for a reptile, particularly that portion constituting the cerebral hemispheres.

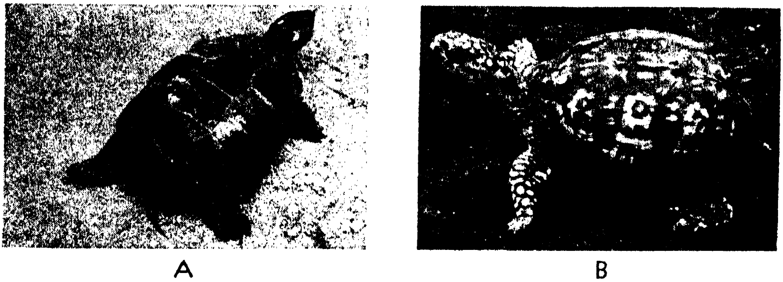


Fig. 56. A, Western painted turtle, *Chrysemys picta dorsalis;* B, Eastern box-turtle, *Terrapene carolina.* (Courtesy N. Y. Zoölogical Society.)

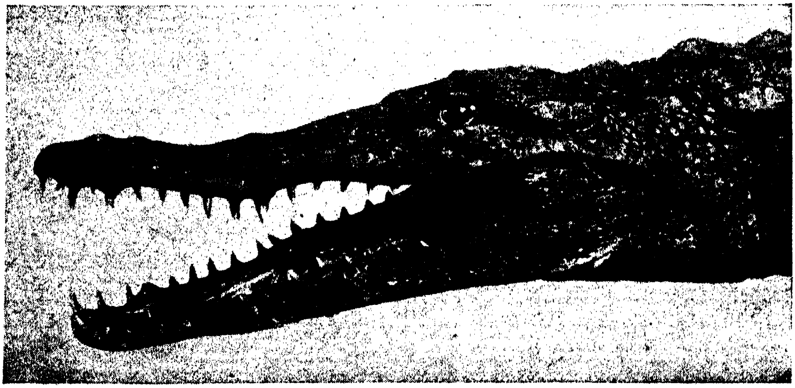


Fig. 57. Head of American crocodile, *Crocodylus acutus.* (Courtesy N. Y. Zoölogical Society.)

The order is represented by four main types which may be conveniently distinguished from one another by the shape of the head. The gavials, *Gavialis gangeticus* of northern India, have an extremely long and slender snout, somewhat like that of *Lepidosteus*. They are confined to India, Borneo, and Sumatra. The crocodiles, of which there are numerous species of the genus *Crocodylus* (Fig. 57), have a long and slender snout which is roughly triangular in outline (Fig. 58B). They have a much wider distribution than the gavials in both the old and the new worlds. The *Caiman* (Fig. 59), of Central and South America, has a more oval or bluntly triangular head. The *Alligator* has a very blunt and rounded snout. *Alligator mississippiensis*, the American form (Fig. 58A), is much larger than the Chinese species, *Alligator sinensis*.

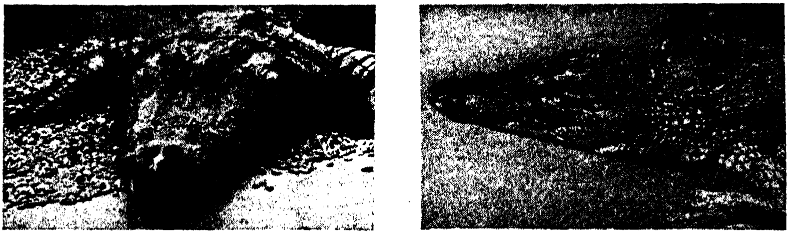


Fig. 58. Heads of American alligator, *Alligator mississippiensis* (A), and American crocodile, *Crocodylus acutus* (B). (Courtesy N. Y. Zoölogical Society.)

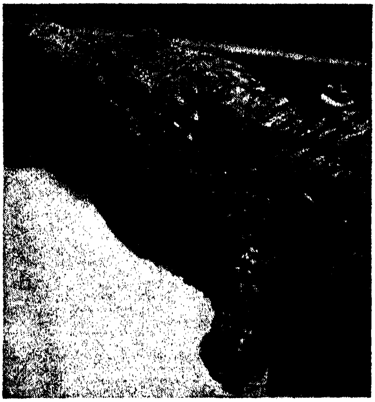


Fig. 59. Spectacled caiman, *Caiman sclerops*. (Courtesy N. Y. Zoölogical Society.)

Squamata—Sauria. Among the lizards we find a wide variety, ranging from large active animals seven or eight feet in length to tiny, wormlike burrowing forms. Although a typical lizard (Fig. 65) differs strikingly from the snakes, they have many characteristics in common. So closely do some of the limbless lizards resemble the snakes, they are often confused. The essential and distinctive features of this suborder in this connection are the presence of eyelids (Fig. 60), the firm union of the two sides of the lower jaw, and the external evidences of an auditory organ. *Varanus komodoensis* (Fig. 61), inhabiting the island of Komodo in the Dutch East Indies, is the largest living lizard, reaching a length of over twelve feet. *Iguana iguana* (Fig. 62) is a large form found in tropical America. *Anolis carolinensis*, one of the new world chameleons, is one of the well-known smaller lizards. *Heloderma suspectum* (Fig. 63), the Gila monster of Arizona and New Mexico, and *Heloderma horridum*, of Mexico and Central America, are the only poisonous lizards known. *Ophisaurus ventralis* (Fig. 64) is a limbless form commonly known as the "glass snake."

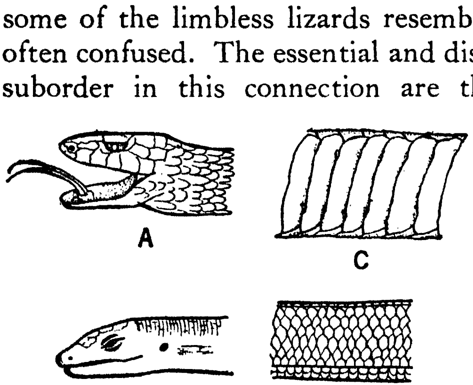


Fig. 60. Head and ventral surface of snake and lizard showing differences. A, head of "copperhead" snake, *Agkistrodon mokasen;* B, head of a legless lizard, *Ophisaurus ventralis*, showing eyelids and external ear opening; C, ventral surface of "copperhead" showing one row of scales; D, ventral surface of *Ophisaurus* showing numerous scales.

Squamata — Ophidia. The snakes also vary greatly in size ranging from a thirty-foot, three-hundred-pound python to small burrowing forms, five or six inches in length. They are more abundant and widely distributed than the lizards, ranging more extensively into temperate regions. They may be described as the most highly specialized of the living reptiles. The absence of limbs in a large majority of snakes is obviously their most distinctive characteristic. Since some of them do possess rudiments of hind limbs, and since, as we have seen, there are certain lizards with absolutely no evidences of such appendages, other characteristics are necessary to definitely separate the two orders. Among such distinctive characteristics may be mentioned the absence of eyelids, the presence of an elastic ligament between the two halves of the lower jaw, and the absence of an external ear.

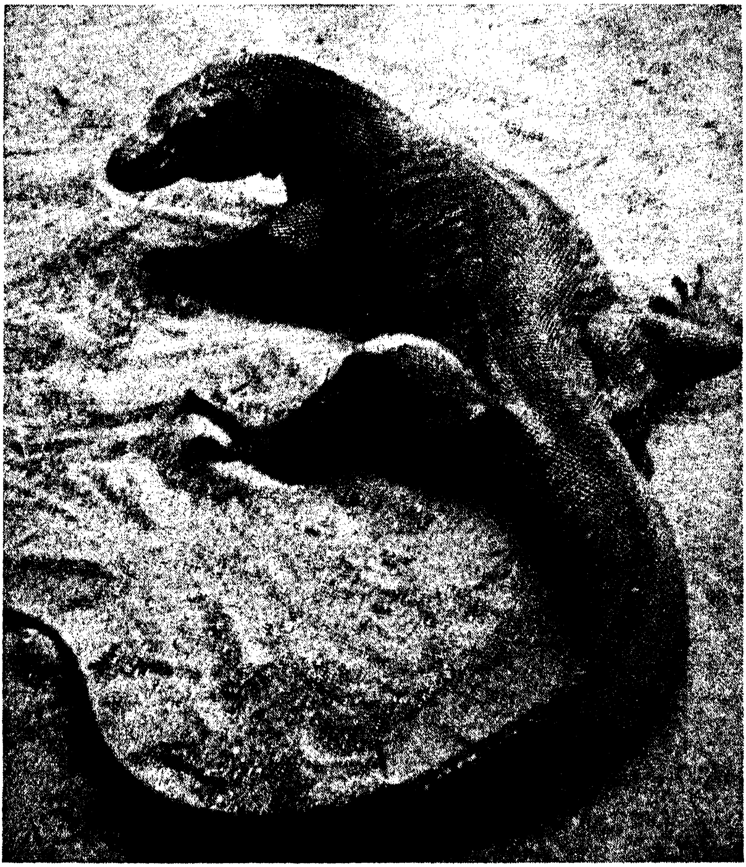


Fig. 61. The giant monitor, *Varanus komodoensis.* (From Ditmars, *Reptiles of the World*, by permission of The Macmillan Company, publishers.)

The snakes as a group have a somewhat bad reputation because of the fact that a few species are venomous. A great majority are not only harmless but are actually beneficial to man in that they destroy large numbers of insects, rodents, and other pests. Of the more common harmless snakes of the

Fig. 62. Common iguana, *Iguana iguana.* (Courtesy N. Y. Zoölogical Society.)

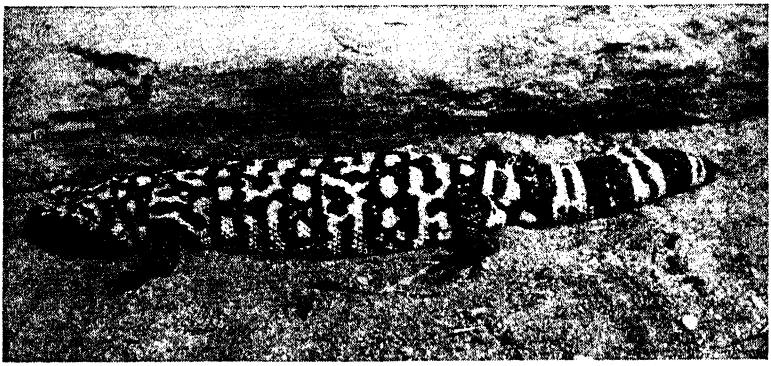


Fig. 63. Gila monster, *Heloderma suspectum.* The only known poisonous lizard in the United States. (From Ditmars, *Reptiles of the World,* by permission of The Macmillan Company, publishers.)

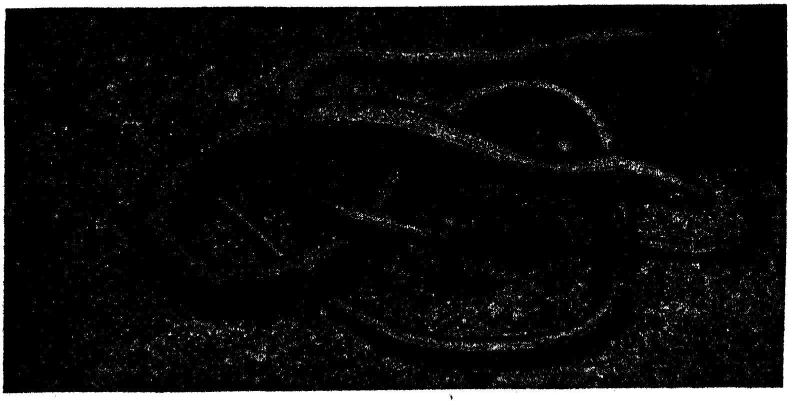


Fig. 64. "Glass snake," *Ophisaurus ventralis.* (Courtesy N. Y. Zoölogical Society.)

United States may be mentioned the various "garter snakes" of the genus *Thamnophis* (Fig. 67), the "black snakes" of the genus *Coluber* (Fig. 68), and several species of "king snakes" of the genus *Lampropeltis* (Fig. 69). The most famous of the poisonous types in North America are *Micrurus fulvius* (Fig. 70), the "coral snake"; *Agkistrodon piscivorus* (Fig. 71), the "water moccasin"; *Agkistrodon mokasen*, the "copperhead"; and *Crotalus adamanteus* (Fig. 72), the "diamondback" rattlesnake. The cobra of India, *Naja naja* (Fig. 73), is perhaps the most notorious of all the poisonous snakes.

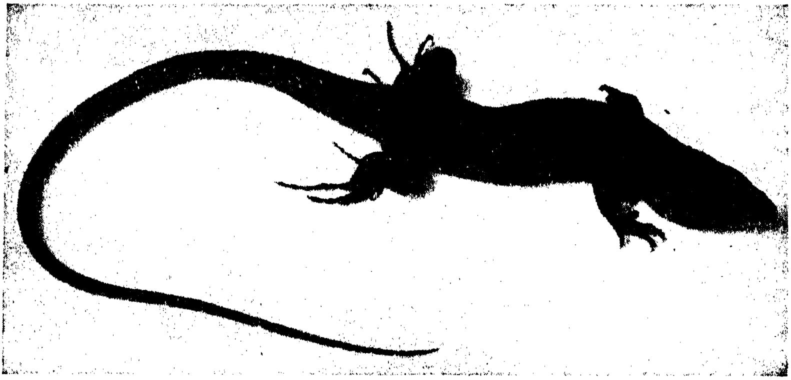


Fig. 65. Green lizard, *Lacerta viridis*. (Courtesy N. Y. Zoölogical Society.)

Fig. 66. Mexican horned "toad," *Phrynosoma orbiculare*. (Courtesy N. Y. Zoölogical Society.)

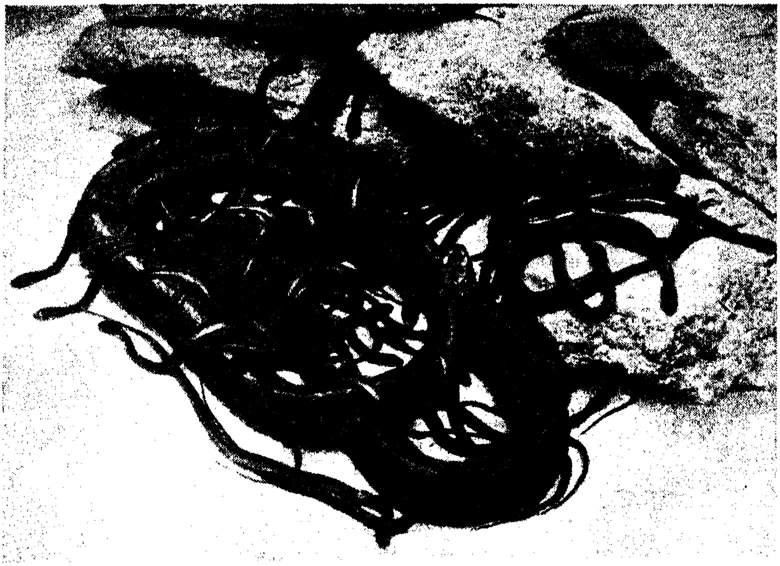


Fig. 67. Common garter snake and young, *Thamnophis sirtalis.* (From Ditmars, *Reptiles of the World,* by permission of The Macmillan Company, publishers.)

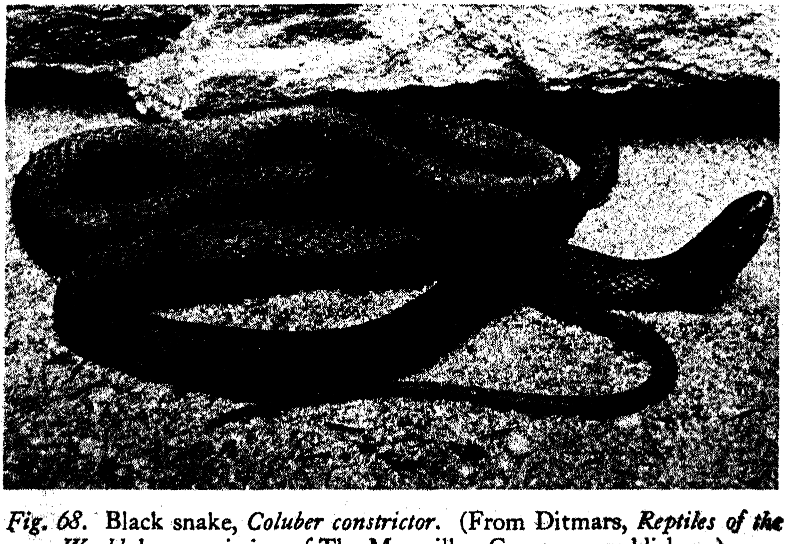


Fig. 68. Black snake, *Coluber constrictor.* (From Ditmars, *Reptiles of the World,* by permission of The Macmillan Company, publishers.)

The largest snake is *Python reticulatus* (Fig. 74), of Burma. This species may reach a length of nearly thirty feet.

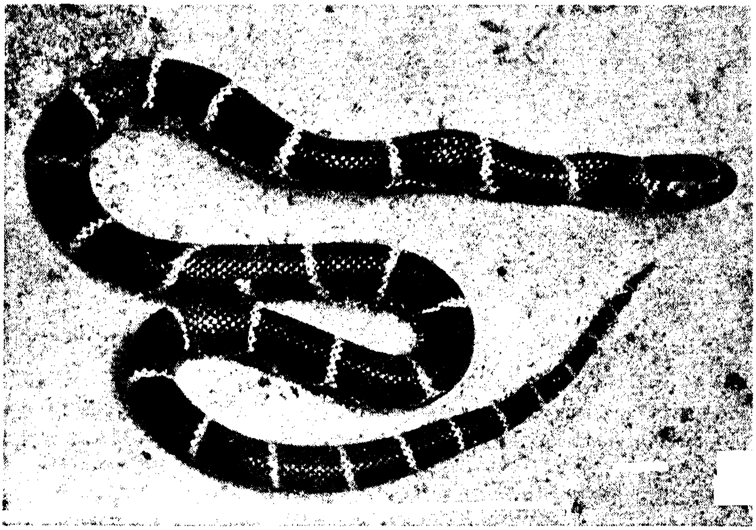


Fig. 69. King snake, *Lampropeltis getulus.* (From Ditmars, *Reptiles of the World*, by permission of The Macmillan Company, publishers.)

✓*Aves*

GENERAL CHARACTERISTICS. The great group of birds contains some of the most highly specialized of living vertebrates. The presence of feathers is sufficient to distinguish them from all other vertebrate classes. In our discussion of the preceding classes, we have emphasized first those modi-

Fig. 70. Florida coral snake, *Micrurus fulvius.* (From Ditmars, *Reptiles of the World*, by permission of The Macmillan Company, publishers.)

fications of structure which have made the fishes the most successful aquatic vertebrates. We saw next in the amphibians the structural experiments which have enabled this

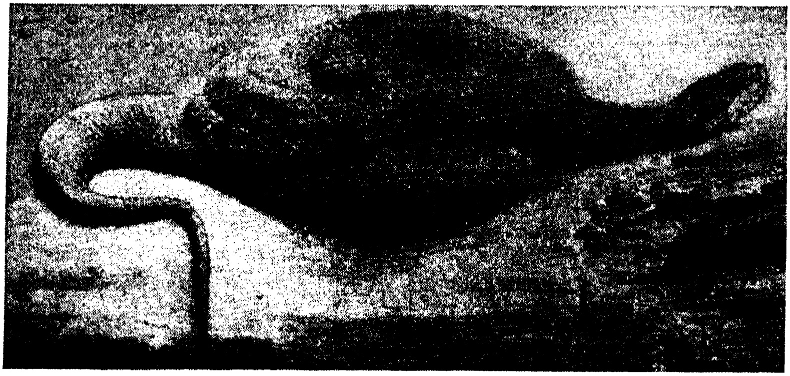


Fig. 71. Water moccasin, *Agkistrodon piscivorus.* (From Ditmars, *Reptiles of the World*, by permission of The Macmillan Company, publishers.)

class at least partially to bridge the gap between a water and a land environment. And finally, in the reptiles, we noted other important modifications which have made them the first thoroughly successful terrestrial forms. The birds now

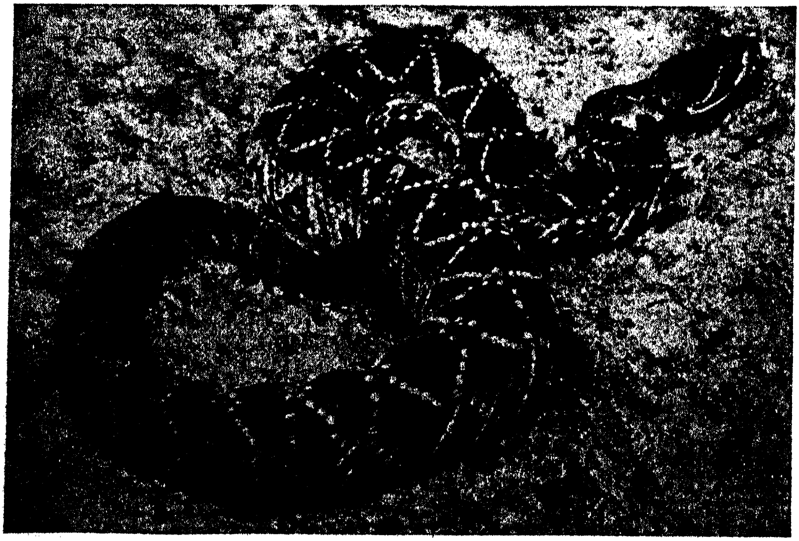


Fig. 72. Diamond-back rattlesnake, *Crotalus adamanteus.* (Courtesy N. Y. Zoölogical Society.)

add the final step in this conquest of possible environments by successfully invading the air.

Although a wide range of adaptations is evident in this class, as is illustrated on the one hand by the numerous semi-aquatic birds, and, on the other, by those forms which are at home under all sorts of conditions on the earth's surface, it is in those modifications which have made possible sustained flight in the air that the birds represent the most notable advance over all other vertebrates. Except for the many features which have made possible long-sustained flight of a heavier-than-air organism, the birds are strikingly similar to the reptiles. In fact, they are often alluded to as "flying" or "glorified reptiles," and some would even include them in the class Reptilia.

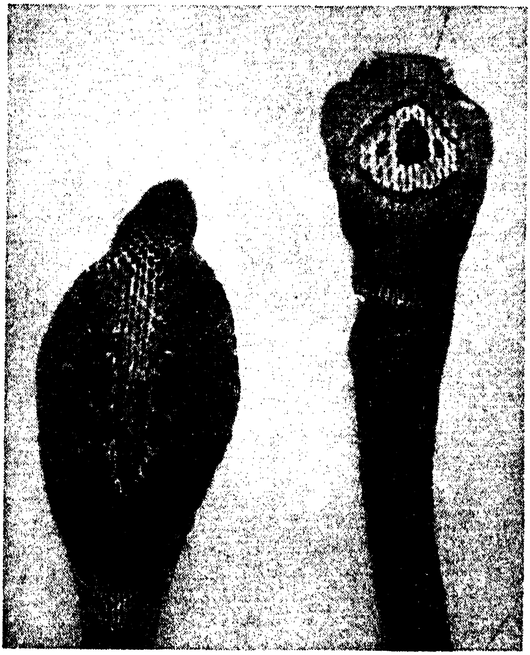


Fig. 73. Head of cobra, *Naja naja.* (From Ditmars, *Reptiles of the World*, by permission of The Macmillan Company, publishers.)

To fly successfully for great distances, a heavier-than-air object must possess at least four characteristic features:

it must be relatively light; it must be strong; it must be equipped with a powerful motor; and it must be provided with steering and balancing devices. The birds have satisfactorily met all of these requirements. Maximum lightness with maximum strength is provided in a number of ways in the body plan of the bird. First, all unnecessary structures have been eliminated or reduced in size. Among these may be mentioned the teeth, which have been lost, and the tail, which has been very much shortened. Many separate bones of the skeleton have been lost and others which remain have been reduced to thin plates or hollowed out and provided with air cavities. The weight caused by the presence of waste materials has been reduced to a minimum by the development of a very efficient digestive system, which provides for rapid and thorough digestion and the frequent elimination of the undigested residue. The presence of numerous air sacs (Fig. 75) in association with the respiratory system serves the additional purpose of making the body more buoyant.

Fig. 74. Regal python, *Python reticulatus.* (Courtesy N. Y. Zoölogical Society.)

The necessary strength of the skeleton is made possible in a number of ways. The vertebrae, with the exception of the cervicals, are firmly united to one another, while the lumbars are fused with the sacrum. The characteristic uncinate processes of the ribs project posteriorly, overlapping the following rib, thus making this part of the skeleton more rigid. A number of architectural principles are noted in the shape of many of the larger bones. When seen in transverse section, the sternum, for example, resembles a T-beam, while other bones, particularly the long bones of the limbs, are constructed on the plan of an I-beam. Such a type of construction gives a maximum of strength and rigidity with the use of a minimum amount of material.

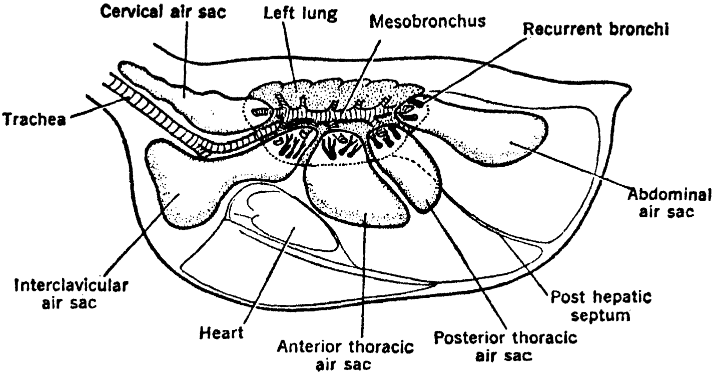


Fig. 75. Diagram of the respiratory organs of a bird, showing accessory air sacs, from the left side. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

Since the bird is provided with a relatively light body supported by a strong skeleton, its next important need is that of efficient motive power. Many of the systems of the bird have contributed directly or indirectly in this connection. The fore limb is the primary locomotor organ. The birds as a class are bipeds, using the hind limbs for locomotion upon the earth's surface or in water, while the fore limbs have been profoundly modified, forming wings for flying. The wing of a bird is supported by a series of bones homologous to those of the fore limb of a typical vertebrate (Fig. 227), but with a greater reduction in the number of phalanges. Operated by a powerful set of breast muscles attached to the keel of the sternum, and provided with numerous feathers which give a planing surface, the wings are most efficient organs of locomotion. Sustaining the weight of the body in the air, to say nothing of driving it onward for surprisingly long distances, requires the expenditure of much energy. Reference has already been made to the efficiency of the digestive system, in the preparation of the required fuel. The respiratory organs are also modified in such a way as to furnish large amounts of oxygen for combustion purposes. The capacity of the lungs is greatly increased by the addition of air sacs (Fig. 75), which branch from them and fill up available spaces in the coelom as well as in the cavities of the long bones. These serve to make available a greater supply of oxygen. Adequate distribution of fuel and oxygen is taken care of by the highly developed circulatory system. The heart itself is four-chambered, thus making possible complete separation of waste-carrying venous blood from oxygen-carrying arterial blood. The capacity of the blood vessels is probably relatively greater than in any other vertebrate. The rate of combustion is also increased by the relatively high temperature which is characteristic of the group. A normal temperature of 110° F. is not at all uncommon in birds. This is maintained by a number of factors, among

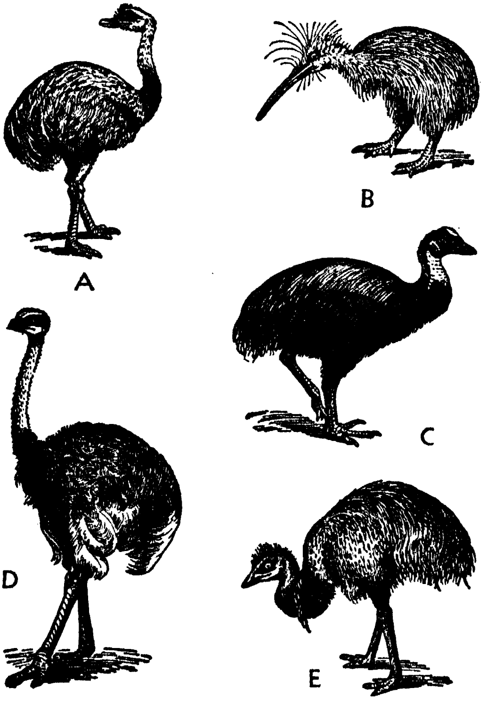


Fig. 76. A series of running birds. A, *Rhea;* B, the kiwi; C, cassowary; D, ostrich; E, emu. (From Newman, *The Phylum Chordata,* redrawn after Evans, by permission of The Macmillan Company, publishers.)

which may be mentioned the efficiency of the circulatory and nervous systems and the presence of the feathers which form an effective non-conducting coat over the surface of the body, thereby preventing loss of heat.

The problem of steering and balancing the bird while in the air is taken care of by the feathers of the tail and by the wings. The tail with its feathers serves as an efficient rudder useful for both horizontal and vertical steering. Balance while gliding is maintained by changes in the position of the wings and of the wing feathers. The great development of those parts of the nervous system which are concerned with equilibration is another influencing character in this connection.

We have thus seen that the body of a bird is highly specialized for flying purposes. Containing all those characteristics which are embodied in the construction of a safe and efficient airplane, it has attained an even higher degree of efficiency than any man-made machine in that it has combined the planing surface as well as the propeller in one structure — the flexible and movable wing.

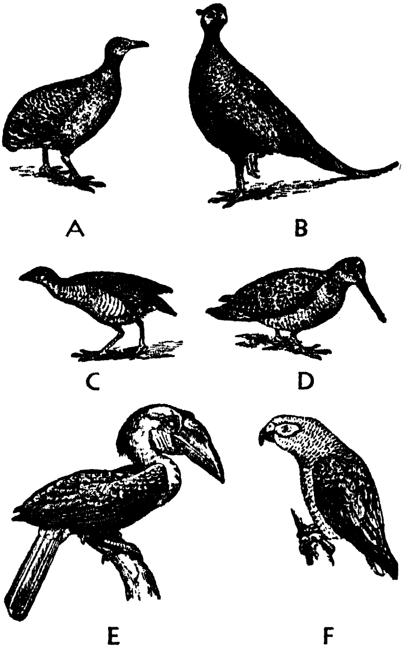


Fig. 77. A series of flying birds. A, great tinamou; B, pheasant; C, land-rail; D, woodcock; E, hornbill; F, parrot. (From Newman, *The Phylum Chordata*, redrawn after Evans, by permission of The Macmillan Company, publishers.)

Other avian characteristics. Among other characteristics common to the birds, the following may be mentioned:

1. A horny beak is present in place of teeth.
2. A third eyelid, or nictitating membrane, is present.

3. The tympanic membrane is withdrawn from the surface and located at the bottom of a short tube, the auditory canal.

4. The aortic arch remains on the right side only.

5. The kidneys are of the metanephric type and are divided into three lobes.

6. There is no urinary bladder.

7. The intestine and the genital and excretory systems empty into a cloaca.

8. Only one ovary and one oviduct, the left, are developed.

9. The cerebellum and the optic lobes are well developed.

CLASSIFICATION. The living birds were formerly divided into two quite well-separated divisions or subclasses — Ratitae, the running birds; and Carinatae, the flying birds. The former division (Fig. 76) included a rather small group of flightless birds characterized by reduced wings and the absence of a keel on the sternum. The other division was a large group of modern flying birds (Fig. 77), most of which are provided with a keel or carina on the sternum, to which are attached the muscles used in flight. Although these terms are little used at the present time by ornithologists, they are of value in a general discussion of the class, which is divided into twenty-five orders.

Order 1. *Struthioniformes.* — Flightless, terrestrial. No keel on sternum. Two toes. The African Ostrich.
Order 2. *Rheiformes.* — Flightless, terrestrial. Three toes. The American Ostrich.
Order 3. *Casuariiformes.* — Flightless, very small wings. Cassowary, Emu.
Order 4. *Crypturiformes.* — Flying, terrestrial. No pygostyle. The Tinamou.
Order 5. *Apterygiformes.* — Flightless, small in size. The Kiwi.
Order 6. *Sphenisciformes.* — Flightless, marine. Paddlelike wings. The Penguin.
Order 7. *Gaviiformes.* — Aquatic, webbed toes. The Loon.
Order 8. *Colymbiformes.* — Aquatic, lobed toes. The Grebe.
Order 9. *Procellariiformes.* — Marine, webbed toes, great power of flight. The Albatross, the Petrel.
Order 10. *Pelecaniformes.* — Aquatic. Toes in most, fully webbed. The Pelican.

Order 11. *Ciconiiformes.* — Long-legged wading birds. The Heron, the Flamingo.
Order 12. *Anseriformes.* — Aquatic, beak covered by soft, sensitive membrane. The Swan, the Goose, the Duck.
Order 13. *Falconiformes.* — Carnivorous birds, curved beaks, sharp claws. The Eagle, the Hawk, the Vulture.
Order 14. *Galliformes.* — Feet adapted for perching. The Pheasant, the Turkey.
Order 15. *Gruiformes.* — Marsh birds. The Rail, the Crane.
Order 16. *Charadriiformes.* — The shore birds. The Plover, the Gull, the Tern.
Order 17. *Columbiformes.* — The Pigeon, the Dove.
Order 18. *Psittaciformes.* — Four toes, two in front and two behind. The Parrot.
Order 19. *Cuculiformes.* — Four toes, two in front and two behind, long tail. The Cuckoo.
Order 20. *Strigiformes.* — Hooked bill, large eyes, sharp claws. The Owl.
Order 21. *Caprimulgiformes.* — The Nighthawk, the Whippoorwill.
Order 22. *Micropodiformes.* — The Swift, the Hummingbird.
Order 23. *Coraciiformes.* — The Kingfisher.
Order 24. *Piciformes.* — The Flicker, the Woodpecker.
Order 25. *Passeriformes.* — A large group of sparrowlike birds, containing more than half of all the known species.

Mammalia

THE POSITION OF THE MAMMALS. The class Mammalia includes a wide variety of forms which are widely distributed in practically all parts of the earth. This wide distribution has been made possible by the efficiency of the various systems which are concerned with maintaining a constant body temperature. Because of this condition of "warm-bloodedness," the mammals as a group are perhaps more independent of environmental changes than any other class of vertebrates, with the possible exception of birds. This independence of climatic changes has made it possible for mammals not only to live successfully in temperate regions, but also to withstand the heat of the tropical deserts or the rigors of an arctic winter.

The mammals are usually thought of as the most highly organized of all animals. This belief is due largely to the commanding position which has been taken by the human mammal, man, in relation to all other types of animals. That man and, to a lesser degree, other mammals have been able to attain such a position has been due to the possession of a well-developed and highly specialized nervous system. The brain, and particularly that portion of it known as the cerebral hemispheres, is more highly developed in mammals than in any other animal. Were it not for this high degree of specialization of the nervous system, other vertebrate classes might have a strong claim for our first consideration, for with respect to the organization of the body as a whole, many of them have gone beyond the mammals.

The wide range of adaptability illustrated in the different members of this class is also of general interest. Many have modifications of structure which enable them to travel swiftly over the earth's surface; some have adaptations for life underground or in burrows; others are adapted for semi-aquatic or even fully aquatic existence; a few enjoy an arboreal habitat; and finally, some have even rivalled the birds in their ability to fly.

CHARACTERISTICS OF THE CLASS. The presence of hair is one of the most apparent characteristics, as distinctive of mammals as feathers are of birds. A majority of forms have a fairly complete covering over the body surface, while in others it is confined to limited regions. All mammals, as the name implies, possess milk-producing glands in the form of modified sweat glands. Sweat and sebaceous glands are also characteristically present in the skin of mammals, the latter type secreting an oily material on the hair shafts. A muscular partition, the diaphragm, separates the thoracic from the abdominal cavity. A well-developed larynx, or voice box, is located at the anterior end of the trachea. The teeth are said to be heterodont, in that they are differentiated into a number of different types, as incisors, canines, premolars, and molars, and are usually diphyodont because there are two sets in life, a milk and a permanent dentition. The mammals resemble the amphibians in having two occipital condyles instead of one, as in the reptiles and birds. The cervical or neck vertebrae are typically seven in number, although in a few species there are six, eight, or nine. The mandible, or lower jaw, consists of a single bone on each side, the dentary, which articulates with the squamosal. There are three auditory bones in the middle ear, the malleus, the incus, and the stapes. The cavities of the bones are filled with bone marrow. With a few exceptions, the coracoid is not present as a separate bone, but is fused to the scapula forming the coracoid process. The red blood corpuscles are circular and non-nucleated. Only one aortic arch, the left, remains. As in the birds, the heart is four-chambered, having two auricles and two ventricles. The external ear is provided with a fleshy cartilaginous lobe, the pinna. The cerebral hemispheres are connected by a heavy commissure, or transverse band of white fibers, known as the corpus callosum. With the exception of the monotremes, the eggs are minute in size and the young are born alive after a relatively long period of development within the uterus. The young are quite helpless at birth and require long periods of parental care and training.

Classification. The classification of the mammals presents a real problem, as there is no simple system that is entirely satisfactory in all respects. The following arrangement of the living forms should be sufficiently complete for a general discussion of the class.

It is convenient first to divide the class into the three subclasses — Prototheria, Metatheria, and Eutheria. The first two of these, Prototheria and Metatheria, contain one order each, while the Eutheria include the remaining orders, which are known as the placental mammals.

Subclass Prototheria

Order *Monotremata*

These are the egg-laying mammals, a small but interesting group containing but three genera, *Proechidna*, *Echidna* (Fig. 78), and *Ornithorhynchus* (Fig. 79). These peculiar forms, found only in Australia and the surrounding islands, differ from other mammals in that they lay eggs. After a period of incubation, the young are hatched and are then nourished by a milklike secretion of modified sweat glands.

Subclass METATHERIA

Order *Marsupialia*

This order includes what are commonly referred to as the "pouched" mammals. A majority of the genera possess an integumentary pouch on the ventral surface. In this pouch the young, which are born in a premature condition, are kept and nourished by true milk. The presence of prepubic bones anterior to the pubis is a characteristic feature. With the exception of a

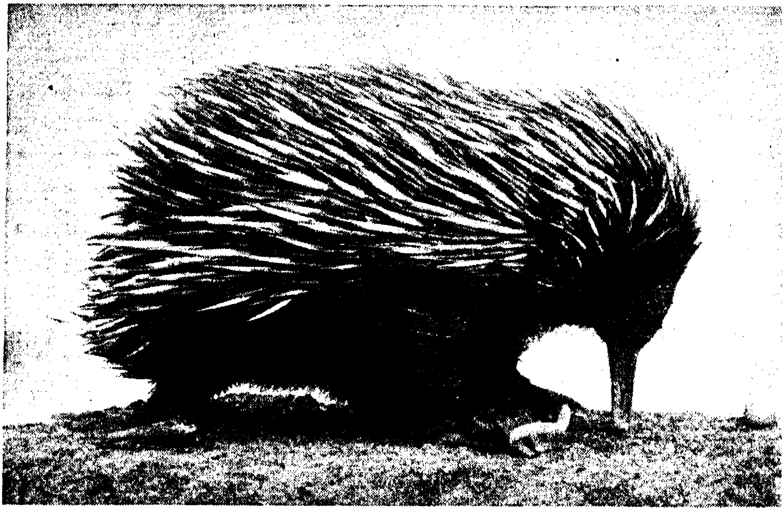


Fig. 78. The spiny anteater, *Echidna.* (Courtesy American Museum of Natural History.)

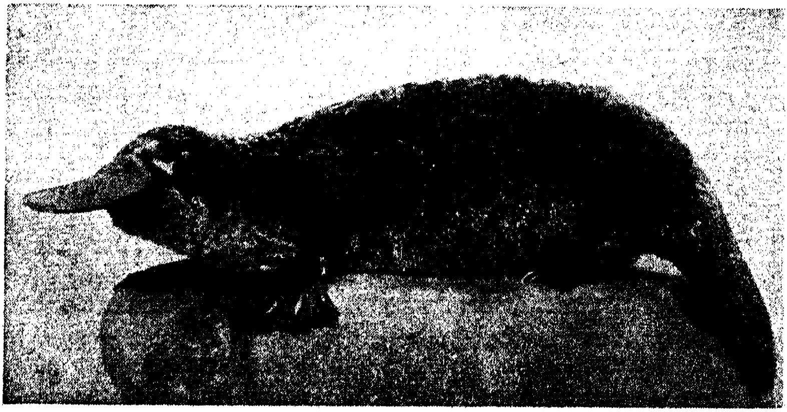


Fig. 79. The duckbill, *Ornithorhynchus anatinus.* (Courtesy American Museum of Natural History.)

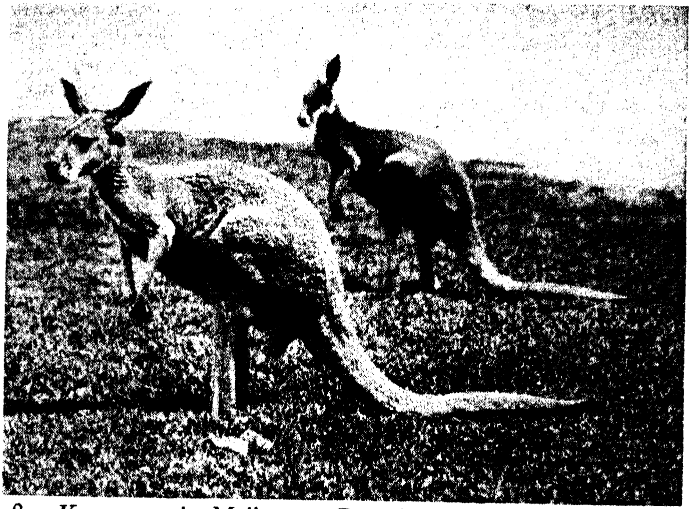


Fig. 80. Kangaroos in Melbourne Zoo, Australia. (Courtesy American Museum of Natural History.)

few genera, the marsupials are confined to Australia and the neighboring regions, where they constitute the native fauna of that part of the world. The most familiar members of this group are the kangaroos (Fig. 80). The exceptions mentioned above are the opossums (*Didelphis*) (Fig. 81), of North, South, and Central America, and the marsupial shrew (*Coenolestes*) of Central America.

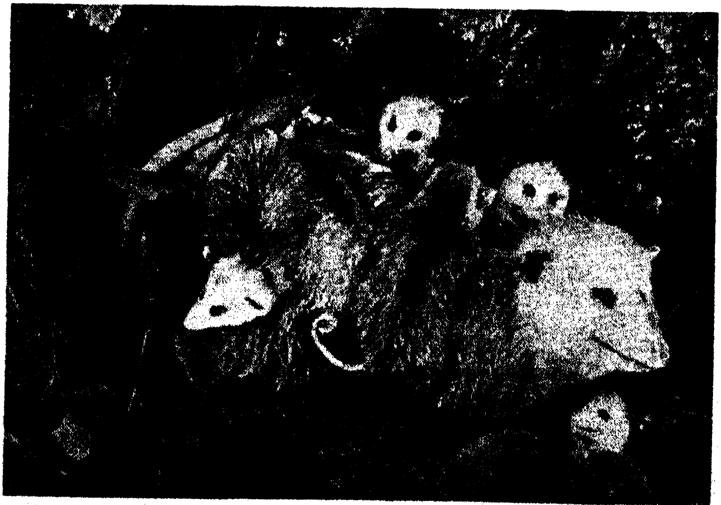


Fig. 81. The common opossum, *Didelphis virginiana.* (Courtesy American Museum of Natural History.)

Subclass Eutheria

This subclass includes a wide variety of mammals which are often referred to as the "placentals" because of the presence of an embryonic structure, the placenta, during foetal life. This subclass may be divided into sixteen distinct orders of living forms.

Order *Insectivora*

The insectivores are relatively small, digging or burrowing mammals with sharp-pointed snouts. They live largely upon insects. The hedgehogs of Europe (*Erinaceus*), the moles (*Scalopus*) (Fig. 82), and the shrews (*Sorex*) are well-known examples.

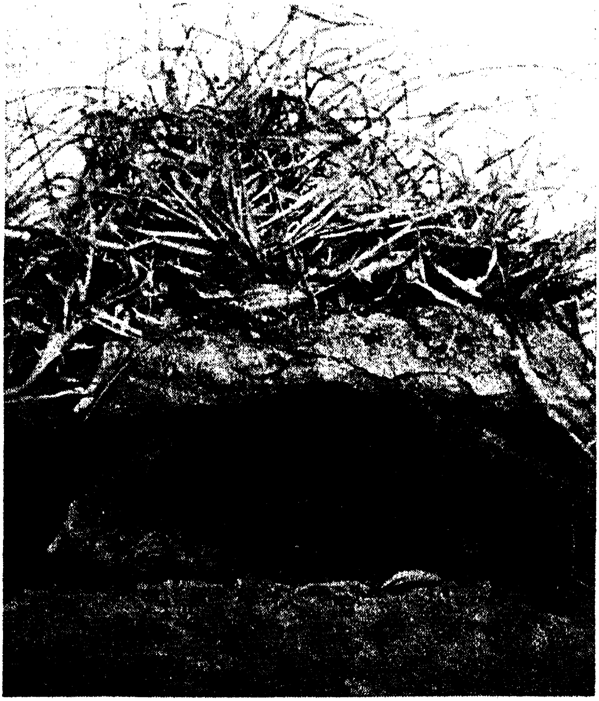


Fig. 82. The common mole, *Scalopus aquaticus.* (Courtesy American Museum of Natural History.)

Order *Dermoptera*

This order includes a single genus, *Galeopithecus* (Fig. 84), the so-called "flying lemur" of Madagascar. Possessing many features in common with the insectivores on one hand and with the bats on the other, this animal is, at the present time, placed in a group by itself between these two orders.

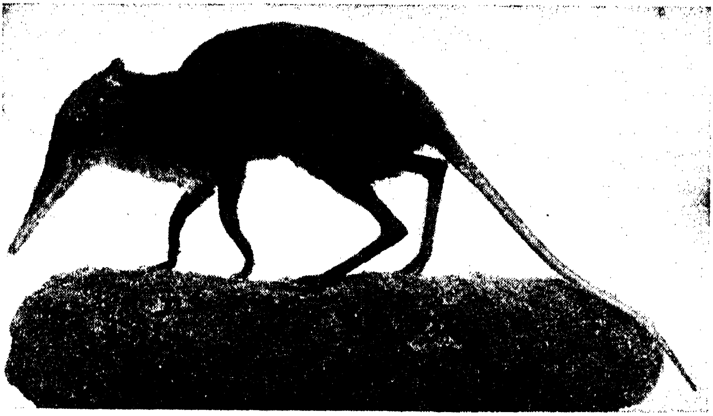


Fig. 83. The giant elephant shrew. (Courtesy American Museum of Natural History.)

Fig. 84. Galeopithecus, the flying lemur. (From Newman, *The Phylum Chordata*, after Vogt and Specht, by permission of The Macmillan Company, publishers.)

Order *Chiroptera*

This order contains about sixty genera of flying mammals or bats. With a fore limb provided with very long digits, and with a web connecting the digits to one another as well as to the sides of the body and even to the hind legs and the tail, these mammals are able to fly quite successfully. Examples are the common brown bat, *Myotis* (Fig. 85), the flying fox, *Pteropus*, and the blood-sucking "vampire" bat, *Desmodus*, of Mexico and South America.

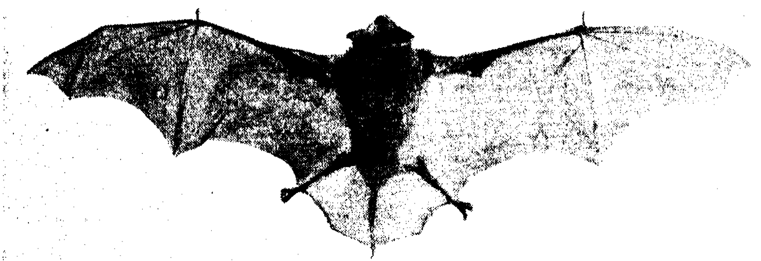


Fig. 85. The brown bat. (Courtesy American Museum of Natural History.)

Order *Primates*

This order of mammals, characterized by the great development of the nervous system, includes thirty-nine genera of lemurs, monkeys (Fig. 86), apes, and man. The primates, as a group, are arboreal forms, with a tendency to assume the bipedal habit in the higher types (Fig. 87). Examples are *Lemur*, the lemur; *Hylobates*, the gibbon; *Cebus*, a new world monkey; and *Homo sapiens*, man.

Order *Edentata*

The members of this order are characterized by having poorly developed teeth, or, in some cases, no teeth. Incisors and canines are usually absent and the other teeth are without enamel. Examples are *Dasypus*, a common armadillo (Fig. 88); and *Bradypus* and *Choloepus*, the sloths (Fig. 89).

Order *Pholidota*

A small group of animals with ant-eating adaptations included in the genus *Manis* (Fig. 91), the scaly anteaters.

Order *Tubulidentata*

This order contains a single genus, *Orycteropus*, the aardvark (Fig. 92), a burrowing mammal of South Africa.

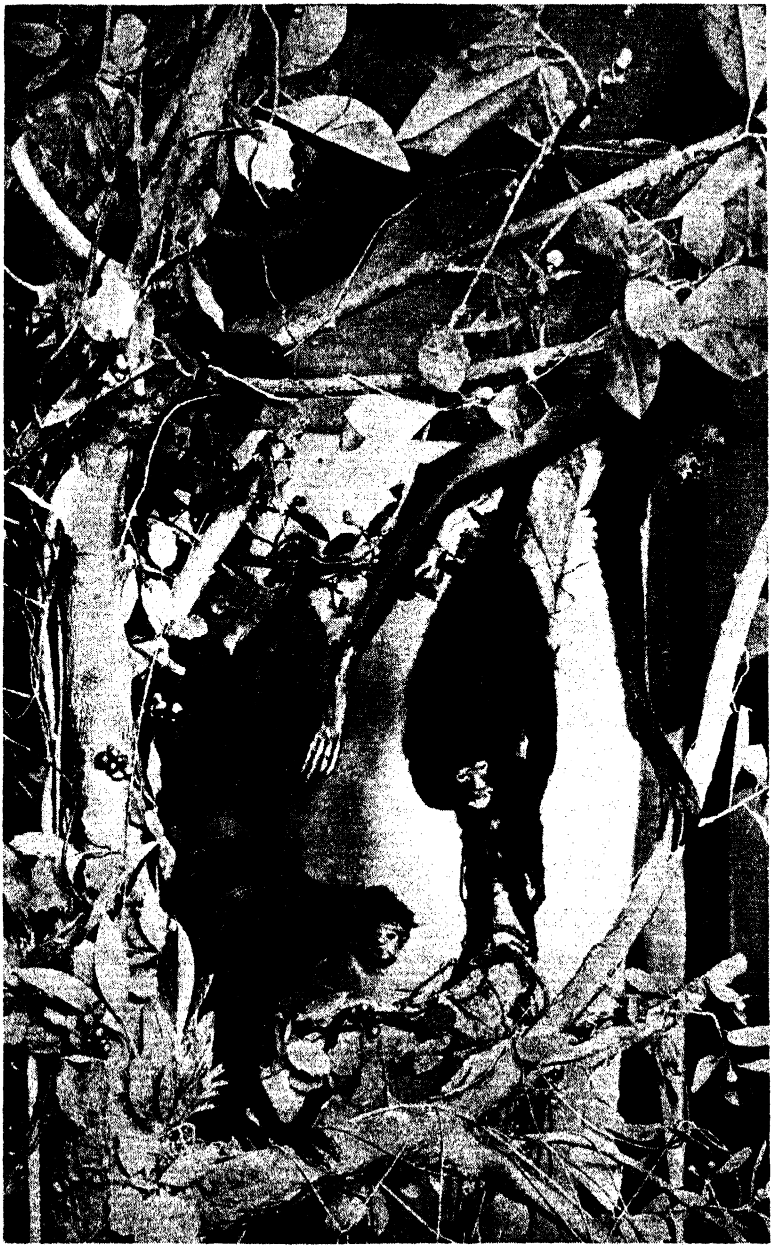


Fig. 86. Spider monkeys. (Courtesy American Museum of Natural History.)

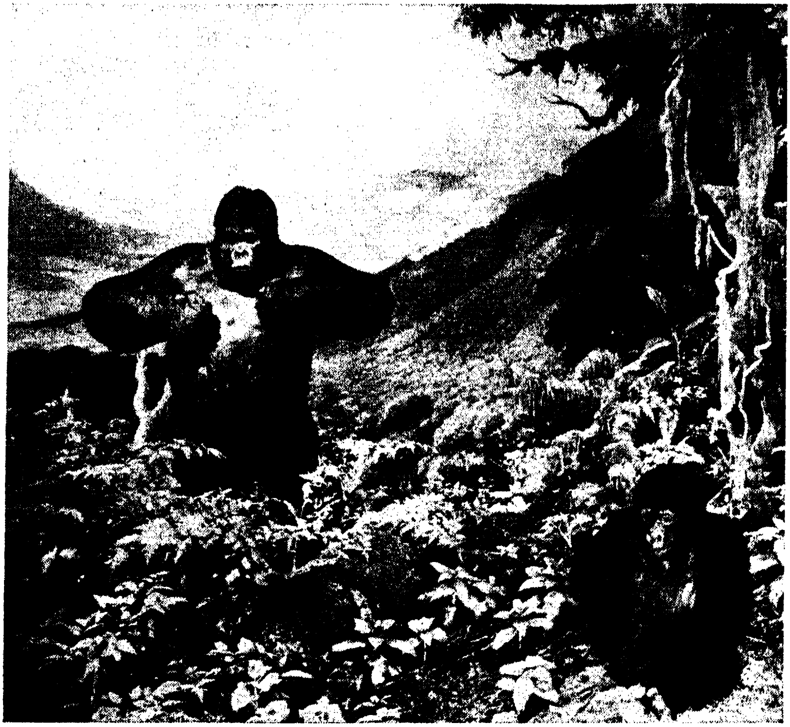


Fig. 87. Gorillas. (Courtesy American Museum of Natural History.)

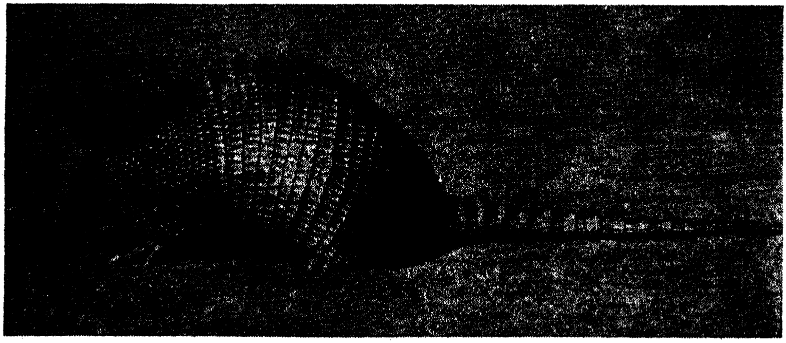


Fig. 88. An armadillo. (Courtesy American Museum of Natural History.)

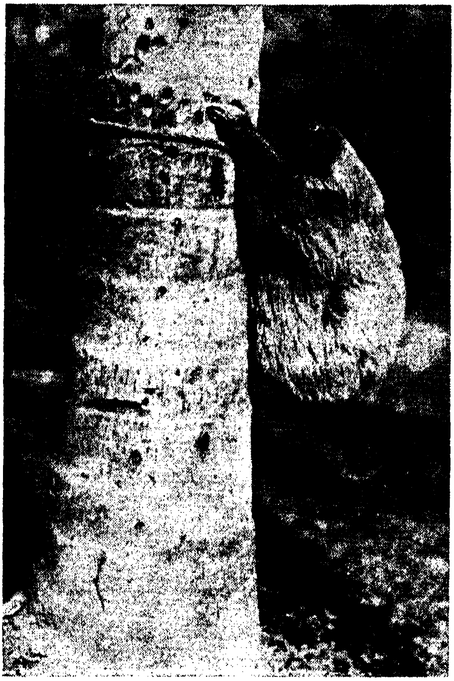


Fig. 89. A sloth. (From photograph by Leo E. Miller, courtesy American Museum of Natural History.)

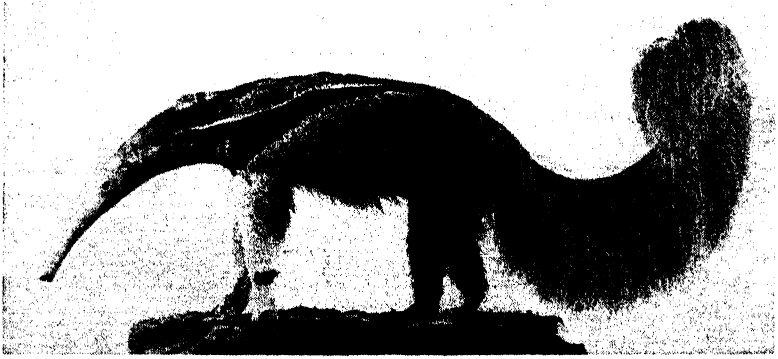


Fig. 90. The great anteater. (Courtesy American Museum of Natural History.)

Order *Rodentia*

This order, containing the gnawing mammals, is the largest in point of numbers, over one hundred genera of living rodents being recognized. For the most part they are small, herbivorous types, without canines and with long, single incisors with chisel-like edges. Among the common genera are *Sciurus*, the squirrel; *Mus*, rats and mice (Fig. 93); *Erethizon*, the porcupine; *Castor*, the beaver; and *Marmota*, the woodchuck.

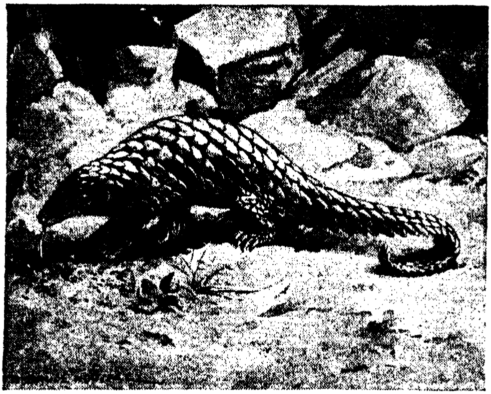


Fig. 91. The pangolin or scaly anteater. (From Hegner, *College Zoology*, by permission of The Macmillan Company, publishers.)

Order *Lagomorpha*

This order contains the rabbits and hares, characterized by the presence of a small second incisor in the upper jaw. Long classi-

Fig. 92. The aardvark. (Courtesy American Museum of Natural History.)

fied as a suborder of rodents, Gidley has given convincing reasons for placing them in a separate group. The typical genus is *Lepus* (Fig. 94).

Order *Carnivora*

The carnivores (Fig. 95), or flesh-eating mammals, are represented by about seventy-five living genera. The order is divided into two distinct suborders — Fissipedia and Pinnipedia. The former contains the land-living forms, including such common animals as the cats, tigers, and lions (Fig. 96), of the genus *Felis;* the dogs, wolves, and coyotes of the genus *Canis;* bears (Fig. 97), genus *Ursus;* and the hyaenas, genus *Hyaena.* The pinnipede carnivores are those flesh-eating mammals which have become secondarily specialized for an aquatic life. Among the representatives are *Phoca*, the seal (Fig. 98); *Odobaenus*, the walrus (Fig. 99); and *Zalophus*, the California sea lion (Fig. 100).

Fig. 93. The field mouse. (Courtesy American Museum of Natural History.)

Order *Cetacea*

The Cetacea, or whales, are the largest living mammals. As a group they are highly specialized for aquatic life, with modified integumentary dorsal fins and fishlike tails. The fore limbs are efficient swimming organs, while the hind limbs have been lost, except for vestiges in certain forms. There are two distinct suborders which might well be given the value of orders, the Denticeti, or toothed whales, and the Mysticeti, the whalebone or toothless whales. The former group includes the smaller forms, such as the dolphin, *Delphinus;* the porpoise (Fig. 101), *Phocaena;* and the sperm whale, *Physeter.* The Mysticeti (Fig. 102) are the larger forms such as *Balaena,* the right whale; and *Balaenoptera,* the hump-backed whale.

Fig. 94. The jack rabbit. (Courtesy American Museum of Natural History.)

Order *Proboscidea*

Hoofed mammals having a long prehensile proboscis. This order contains the mammoths, mastodons, and elephants, of which there are two living genera, *Elephas* of Asia and *Loxodonta* of Africa (Fig. 103). These are the largest living land animals.

Order *Hyracoidea*

This is a small group containing a single genus *Procavia* (Fig. 104), the coneys of Syria and Arabia. Small animals resembling guinea pigs, they are provided with hooflike digital tips.

Order *Sirenia*

This order includes but two genera, *Halicore,* the dugong (Fig. 105), and *Trichechus,* the manatee, commonly known as sea cows from their habit of feeding upon sea weeds. They have flipperlike fore limbs, a fishlike tail, and other aquatic modifications. The hind limbs are entirely missing.

Order *Perissodactyla*

The odd-toed, hoofed mammals (Fig. 106). This order includes the horse, *Equus;* the tapir, *Tapirus;* and the rhinoceros, *Rhinoceros* (Fig. 107).

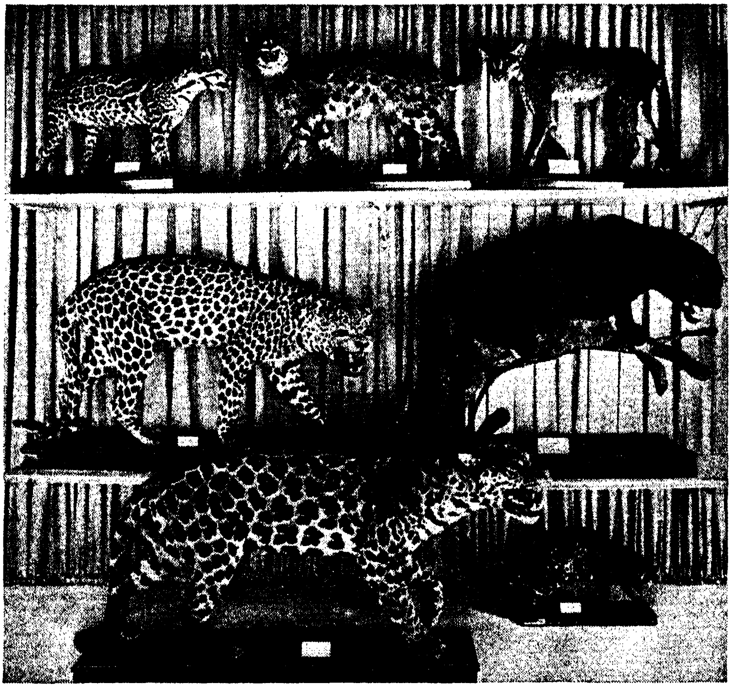


Fig. 95. A series of carnivores. (Courtesy American Museum of Natural History.)

Order *Artiodactyla*

This group contains the even-toed (Fig. 108), hoofed mammals including the swine, *Sus;* the hippopotami, *Hippopotamus;* the camels and dromedaries, *Camelus;* the American bison, *Bison;* domestic cattle, *Bos;* the giraffe, *Giraffa* (Fig. 109); and many genera of deer and antelopes.

SUMMARY

The relation of the different vertebrate groups to one another must be understood before one can intelligently study their comparative morphology. The arrangement of vertebrates in an orderly manner is known as classification or taxonomy.

There are seven classes of vertebrates, each of which may be further subdivided into smaller groups such as orders, families, and genera. A genus may contain a number of species. The scientific name consists of the name of the genus and species.

Fig. 96. The African lion, *Felis leo*. (Courtesy American Museum of Natural History.)

The classification of the vertebrates as described at length in the preceding pages may be briefly summarized as follows:

CLASS I. AGNATHA — Aquatic, no lower jaw, round mouth, no paired appendages, no scales.
  Order *Cyclostomata* — Contains the living members of the class.
    Suborder 1. *Myxinoidea* — Nostril terminal, communicating with pharynx.

Fig. 97. Polar bears. (Courtesy American Museum of Natural History.)

Genus. (a) *Bdellostoma* — Pacific hagfish.
(b) *Myxine* — Atlantic hagfish.
Suborder 2. *Petromyzontia* — Nostril more dorsal, ending blindly.
Genus. *Petromyzon* — The lamprey.

Fig. 98. Alaska fur seals. (Courtesy American Museum of Natural History.)

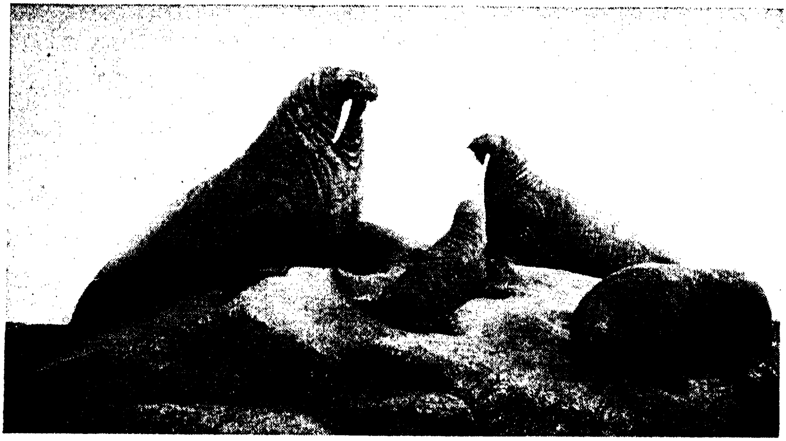


Fig. 99. Walruses. (Courtesy American Museum of Natural History.)

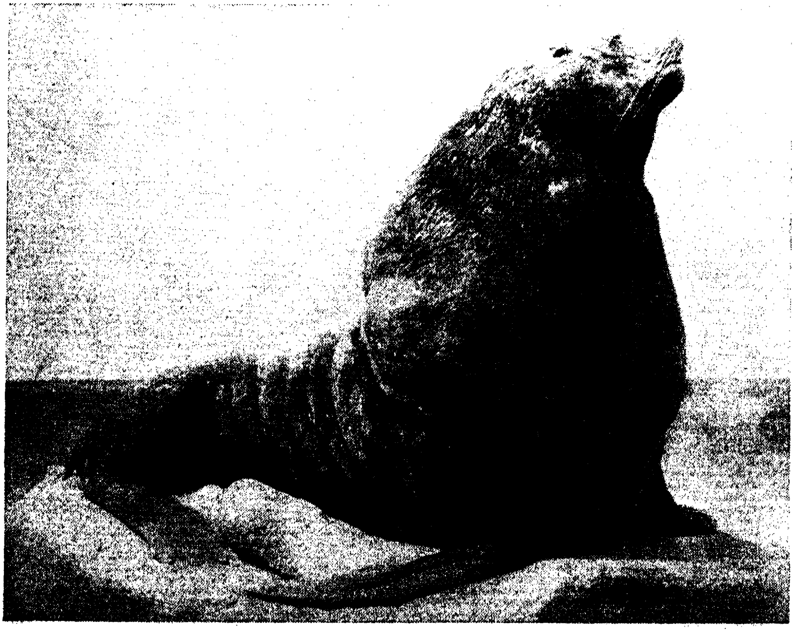


Fig. 100. The Steller sea lion. (Courtesy American Museum of Natural History.)

Class II. Chondrichthyes — Aquatic, paired fins, cartilaginous skeleton, movable lower jaw, usually placoid scales, ten pairs of cranial nerves.

Order A. *Elasmobranchii* — Open gill slits, heterocercal tail, placoid scales, spiral valve, cloaca.

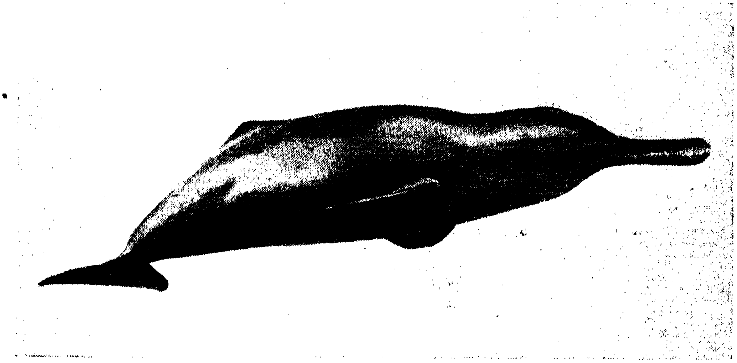


Fig. 101. The porpoise. (Courtesy American Museum of Natural History.)

Genus. (a) *Squalus* — Spiny dogfish with spines on dorsal fins.
(b) *Raia* — The rays, dorsoventrally flattened.

Order B. *Holocephali* — Beginnings of operculum, teeth are crushing plates, no cloaca.

Genus. *Chimaera* — The ratfish.

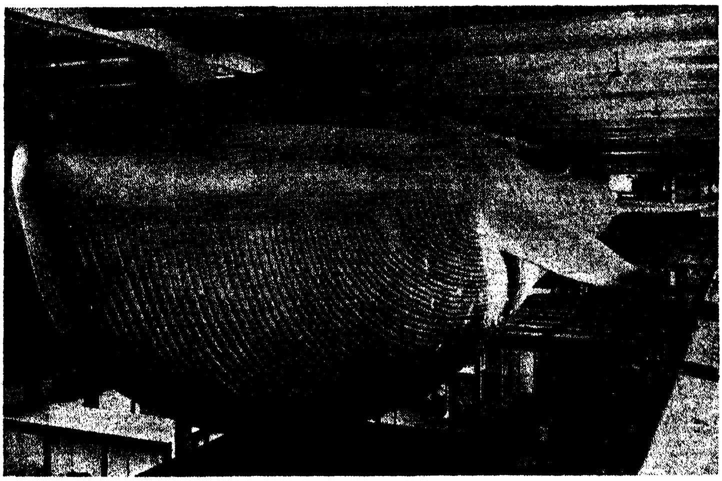


Fig. 102. The sulphur-bottom whale. (From photograph of model, courtesy American Museum of Natural History.)

Class III. Osteichthyes — Aquatic, paired fins, chiefly a bony skeleton. Ganoid, cycloid, or ctenoid scales. Operculum and air bladder present. No claspers.

Subclass 1. *Choanichthyes* — Internal nostrils present. Lobe fins. Air bladder used as lung.

Order A. *Crossopterygii* — Ganoid scales, lobe fins, jaw suspension hyostylic, spiracle present.

Genus. *Latimeria* — The only known living representative.

Order B. *Dipnoi* — No spiracle. Jaw suspension autostylic, tooth plates, spiral valve.

Genus. (a) *Protopterus* — The African lungfish.
(b) *Epiceratodus* — The Australian lungfish.
(c) *Lepidosiren* — The South American lungfish.

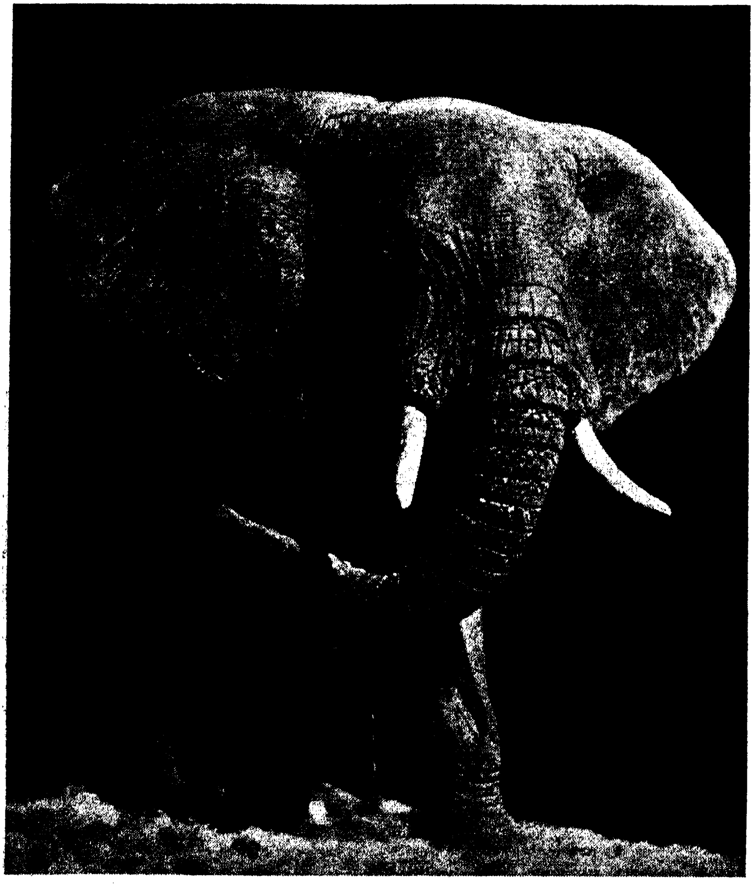


Fig. 103. The African elephant. (Courtesy American Museum of Natural History.)

Subclass 2. *Actinopterygii* — No internal nostrils. Fin rays attached directly to girdles. Jaw suspension hyostylic. No cloaca.

Order A. *Chondrostei* — Skeleton mainly cartilaginous. Spiral valve present, ganoid scales.

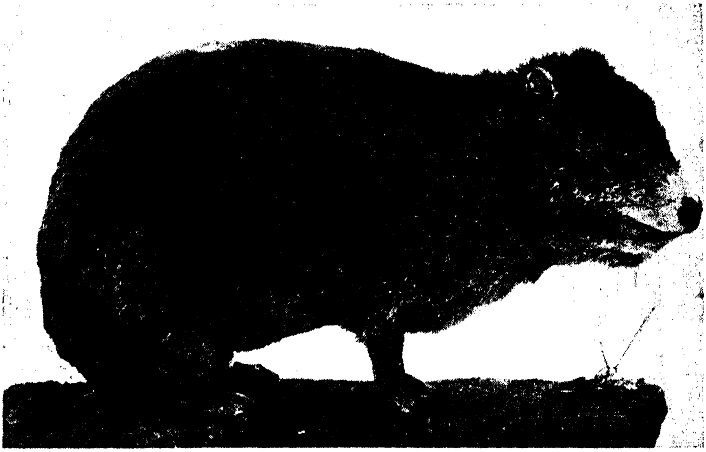


Fig. 104. The coney. (Courtesy American Museum of Natural History.)

Suborder. *Polypterini* — Pectoral fins with basal lobes. Lungs open ventrally.

Genus. *Polypterus* — Of the Nile.

Suborder. *Acipenseroidea* — Tail heterocercal. Lung opens dorsally.

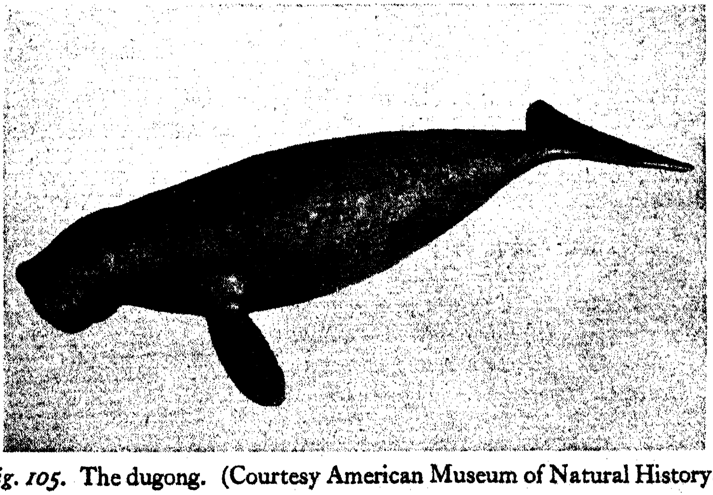


Fig. 105. The dugong. (Courtesy American Museum of Natural History.)

Genus. (a) *Acipenser* — The common sturgeon.
(b) *Polyodon* — The paddlefish.

Order B. *Holostei* — Skeleton largely of bone. Single air bladder opens dorsally, and is used as a lung.

Suborder. *Lepidosteoidei* — Tilelike ganoid scales.

Genus. *Lepidosteus* — The North American garpike.

Suborder. *Amioidei* — Continuous dorsal fin. Large cycloid scales.

Genus. *Amia* — The "bow-fin."

Order C. *Teleostei* — The typical bony fishes. Scales cycloid or ctenoid. Single dorsal air bladder. Tail usually homocercal.

Genus. (a) *Scomber* — The mackerel.
(b) *Perca* — The perch.
(c) *Ameiurus* — The catfish.

Class IV. Amphibia — Partly aquatic and partly terrestrial. Larval life in a liquid or moist medium, tetrapod limbs, two occipital condyles, no claws or scales, ten pairs of cranial nerves.

Order A. *Gymnophiona* — Legless, burrowing.

Genus. *Caecilia* — The "blind-worm."

Order B. *Caudata* — With tails in the adult.

Genus. (a) *Necturus* — Permanently aquatic.
(b) *Amphiuma* — Eel-like, small limbs.
(c) *Plethodon* — Lungless.
(d) *Triturus* — The newt.

Order C. *Salientia* — Tailless in the adult.

Genus. (a) *Rana* — The frogs.
(b) *Hyla* — The tree toads.
(c) *Bufo* — The toads.

Class V. Reptilia — Terrestrial, scales, claws, amnion and allantois, one occipital condyle, twelve pairs of cranial nerves.

Order A. *Rhynchocephalia* — Primitive third eye (pineal).

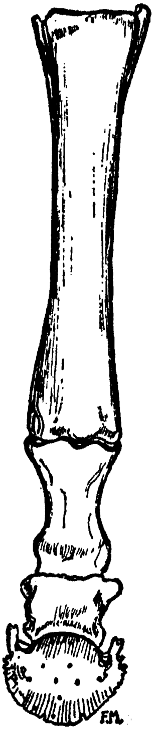


Fig. 106. Foot of horse, *Equus caballus*, order Perissodactyla.

Genus. *Sphenodon* — Only living genus.

Order B. *Chelonia* — Boxlike covering of scales and bony plates.

Genus. (a) *Chelydra* — Snapping turtle.
(b) *Chrysemys* — Painted turtle.
(c) *Terrapene* — Box tortoise.

Order C. *Crocodilia* — Four-chambered heart.

Genus. (a) *Crocodylus* — The crocodile.
(b) *Alligator* — The alligator.

Order D. *Squamata* — Lizards and snakes.

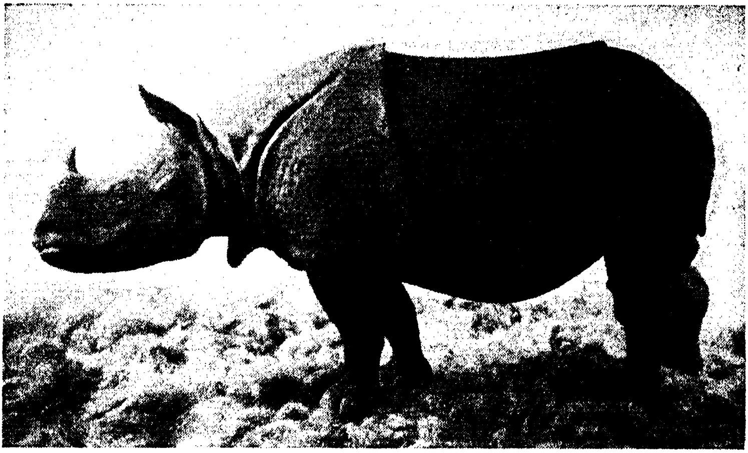


Fig. 107. The Asiatic rhinoceros. (Courtesy American Museum of Natural History.)

Suborder *Sauria*. Movable eyelids, external ear opening, halves of lower jaw firmly united.

- Genus. (a) *Anolis* — The new world chameleon.
  - (b) *Heloderma* — The Gila monster.
  - (c) *Iguana* — The common iguana.

Suborder *Ophidia*. Without movable eyelids, no external ear, halves of the lower jaw held together by elastic ligament.

- Genus. (a) *Thamnophis* — The garter snake.
  - (b) *Coluber* — The black snake.
  - (c) *Crotalus* — The rattlesnake.

CLASS VI. AVES — Feathers, fore limbs are modified as wings, bipedal, claws on hind limb, one occipital condyle. (The orders of living birds have been previously given in the form of a summary. See pages 82–83.)

CLASS VII. MAMMALIA — Warm-blooded, hair, mammary glands.

- Subclass 1. *Prototheria* — Egg-laying.
  - Order A. *Monotremata*
    - Genus. (a) *Ornithorhynchus* — The duckbill.
    - (b) *Echidna* — The spiny anteater.
- Subclass 2. *Metatheria* — Usually with a pouch.
  - Order B. *Marsupialia*
    - Genus. (a) *Didelphis* — The opossum.
    - (b) *Macropus* — The kangaroo.

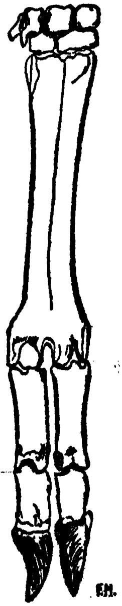


Fig. 108. Foot of goat, *Capra liveus*, order Artiodactyla.

Subclass 3. *Eutheria* — Placental mammals.
  Order C. *Insectivora* — Small, terrestrial, plantigrade.
    Genus. (a) *Erinaceus* — The hedgehog.
      (b) *Scalopus* — The mole.
      (c) *Sorex* — The shrew.
  Order D. *Dermoptera* — Flying (gliding) forms.
    Genus. *Galeopithecus* — The flying lemur.
  Order E. *Chiroptera* — True flying mammals.
    Genus. (a) *Desmodus* — The vampire bat.
      (b) *Myotis* — The brown bat.

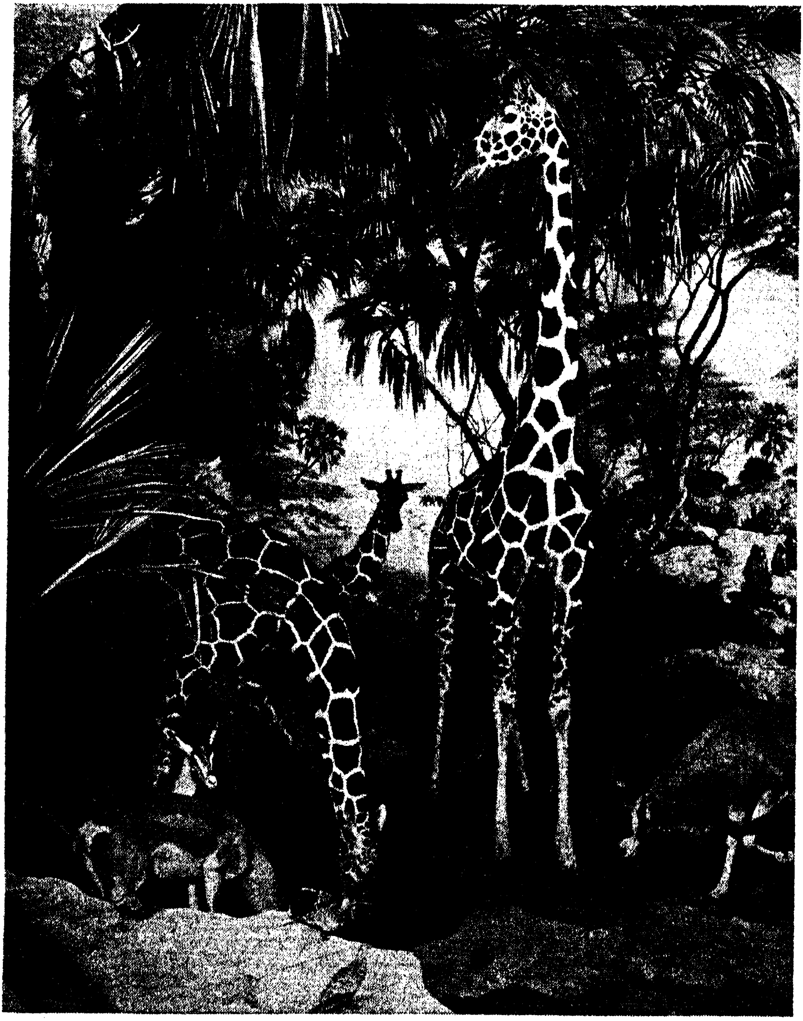


Fig. 109. The giraffe. (Courtesy American Museum of Natural History.)

Order F. *Primates* — Highly developed nervous system, bipedal tendencies.
  Genus. (a) *Lemur* — The lemur.
    (b) *Cebus* — The capuchin.
    (c) *Gorilla* — The gorilla.
    (d) *Homo* — Man.
Order G. *Edentata* — Teeth without enamel.
  Genus. (a) *Bradypus* — The three-toed sloth.
    (b) *Dasypus* — The armadillo.
Order H. *Pholidota* — Scaly anteater.
  Genus. *Manis* — The pangolin.
Order I. *Tubulidentata* — A single genus in South Africa.
  Genus. *Orycteropus* — The aardvark.
Order J. *Rodentia* — Gnawing mammals, large single incisors.
  Genus. (a) *Sciurus* — The squirrel.
    (b) *Castor* — The beaver.
    (c) *Erethizon* — The porcupine.
Order K. *Lagomorpha* — Two pairs of incisors in the upper jaw.
  Genus. *Lepus* — The rabbit.
Order L. *Carnivora* — Flesh-eating, large canines.
 Suborder *Fissipedia* — Land-living.
  Genus. (a) *Felis* — The cats.
    (b) *Canis* — The dogs.
    (c) *Ursus* — The bears.
 Suborder *Pinnipedia* — Water-living.
  Genus. (a) *Phoca* — The seal.
    (b) *Odobaenus* — The walrus.
    (c) *Zalophus* — The sea lion.
Order M. *Cetacea* — Fully aquatic.
 Suborder *Denticeti* — Toothed whales.
  Genus. *Phocaena* — Sperm whale.
 Suborder *Mysticeti* — Toothless whales.
  Genus. *Balaena* — The right whale.
Order N. *Proboscidea* — With prehensile proboscis.
  Genus. *Elephas* — The Asiatic elephant.
Order O. *Hyracoidea* — Small rodentlike forms.
  Genus. *Procavia* — The coney.
Order P. *Sirenia* — Fully aquatic.
  Genus. (a) *Halicore* — The dugong.
    (b) *Trichechus* — The manatee.
Order Q. *Perissodactyla* — Odd-toed ungulates.
  Genus. (a) *Equus* — The horse.
    (b) *Tapirus* — The tapir.
    (c) *Rhinoceros* — The rhinoceros.

Order R. *Artiodactyla* — Even-toed ungulates.
  Genus. (a) *Bos* — Domestic cattle.
    (b) *Camelus* — The camel.
    (c) *Sus* — The pig.
    (d) *Giraffa* — The giraffe.

V. Early Vertebrate Development

Before discussing the morphology of the various vertebrates, it seems desirable to give a brief account of the early stages of development of the vertebrate body. Although there is much variation in details in the different classes, it is possible to give a general description of the changes which take place. In this chapter we shall consider only the earlier changes, leaving an account of the formation of the various organs to the following chapters, which deal with the systems of which the organs are a part.

THE GERM CELLS. The body of any vertebrate has resulted from a series of cell divisions which followed the union of two germ cells (female and male) — the egg and the sperm. Although differing greatly from each other, both kinds of germ cells are derived from cells which are similar in the two sexes, and which are known as primordial germ cells. After a period of multiplication by ordinary mitotic divisions, followed by a period of growth, the germ cells are further prepared by what is known as maturation (Fig. 110).

Maturation. The maturation divisions differ from ordinary mitosis in that in one of them the chromosomes do not divide and separate in the usual manner. After coming together in pairs, thereby forming double chromosomes, each chromosome splits longitudinally. This results in the formation of a group of four half-chromosomes, known as a tetrad. In a subsequent division, the chromosomes which formed the original pair, each of which now consists of two half-chromosomes, separate from one another. This division, then, is essentially a separation of two chromosomes which have previously come together to form a pair. It differs from the chromosome division in a typical mitosis in which the members of a chromosome pair individually split lengthwise, the four resulting half-chromosomes remaining separated.

As a result of the maturation divisions, the new cells formed have one half the number of chromosomes characteristic of the species. The significance of this process will be apparent when fertilization, the union of the male and female germ cells, is considered. The other maturation division is a typical mitotic division.

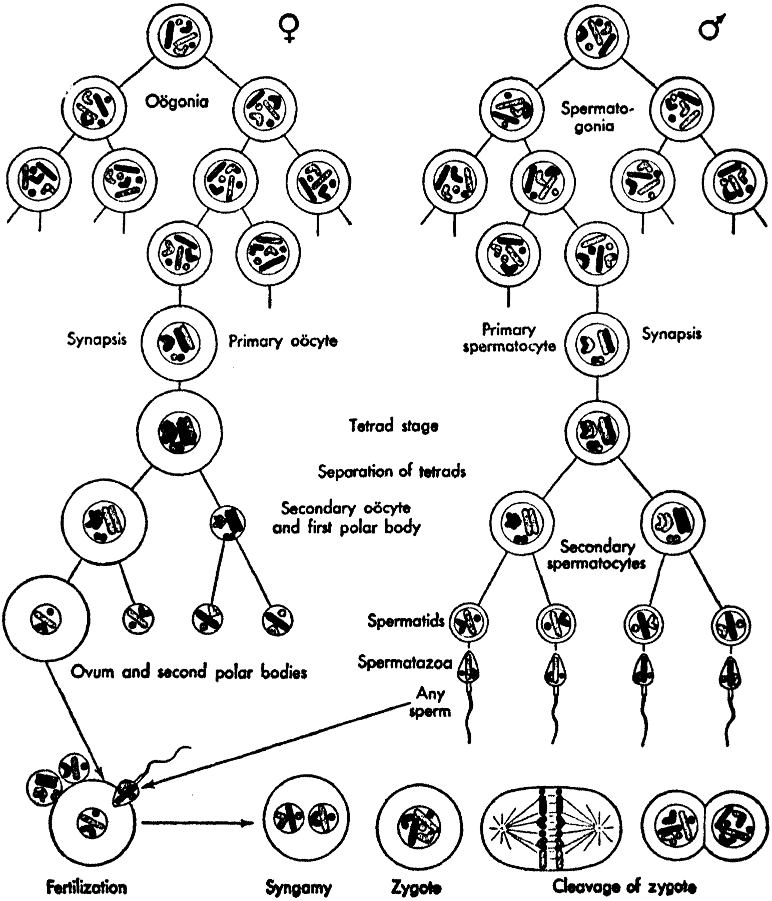


Fig. 110. Scheme of oögenesis, spermatogenesis, fertilization, and cleavage. (From Huettner, *Fundamentals of the Comparative Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

The behavior of the nucleus during the maturation divisions is essentially the same in the two sexes, while the division of the cytoplasm differs greatly. In the male germ cell, the cytoplasm is divided equally, so that as a result of maturation there develop, from each primary spermatocyte, four mature germ cells which are equal in respect to their cytoplasmic content as well as to their nuclear material. These four cells, which are first known as spermatids, do not divide further, but undergo a striking metamorphosis during which they take on the form of the fully developed spermatozoa characteristic of the species.

In the case of the female germ cell, the cytoplasm divides unequally at each maturation division. The first division results in the formation of one large and one small cell. The latter, which has the same chromosome content but very little cytoplasm, is known as the first polar body. At the second division of the larger cell, two unequal cells are again formed, the smaller being the second polar body. The first polar body may also divide, but it plays no further part in the development of the female germ cell. The second polar body is also a nonfunctional cell, and both the first and second polar bodies soon degenerate. These preparatory divisions have, therefore, resulted in the formation of a single mature female germ cell and two or three polar bodies. The cell thus matured also undergoes a period of metamorphosis or growth as a result of which it becomes an ovum of the type characteristic of the species.

The structure of the spermatozoon. The male germ cell of the vertebrates differs in many important respects from the female cell. It is a much smaller unit, and is without yolk or other reserve food materials. Provided with a flagellum or tail, it is capable of locomotion and thus may reach the stationary ovum. A typical spermatozoon (Fig. 111) consists mainly of three parts, the head, middle piece, and tail. The former is made up almost entirely of the nucleus with a pointed body, the acrosome, or perforatorium, just anterior to it. It was formerly believed that the acrosome is used in piercing the surface of the ovum at the time of fertilization.

The tail consists of a central axial filament surrounded for a greater part of its length by a sheath of cytoplasm. The axial filament begins in a centrosome located just posterior to the nucleus and in some forms even embedded in it. A varying number of centrosomes may be located along the axial filament posterior to the one in which it begins. The size and shape of the spermatozoa and of their various parts are subject to much variation in the different vertebrates (Fig. 112).

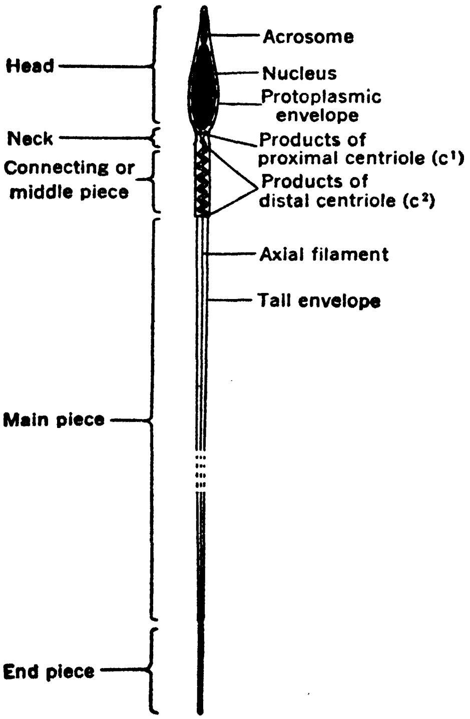

Head
Neck
Connecting or middle piece
Main piece
End piece
Acrosome
Nucleus
Protoplasmic envelope
Products of proximal centriole (c¹)
Products of distal centriole (c²)
Axial filament
Tail envelope

Fig. 111. Diagram of animal sperm, based on the conditions found in mammals. A long section of the flagellum, indicated by dotted lines, is omitted. (From Wilson, *The Cell in Development and Heredity*, by permission of The Macmillan Company, publishers.)

The structure of the ovum. The egg is a relatively large cell incapable of locomotion. The shape is typically spherical, although often slightly elliptical or ovoid (Fig. 113). The size varies greatly in the different classes of vertebrates, depending upon the amount of reserve food material, or yolk, which the eggs contain. In the oviparous forms generally, it is very large, while in the placental mammals it is very small. The vertebrate ovum is said to be telolecithal when the yolk or deutoplasm is concentrated at one side of the egg and the cytoplasm at the opposite side. The eggs of many non-chordates are homolecithal, that is, having the yolk more generally distributed throughout the egg. An ovum with a small amount of yolk present is said to be of the microlecithal type, while one with a large amount of yolk is megalecithal. The egg of placental mammals (Fig. 114) is of the former type and the egg of a bird of the latter. In the egg of a hen (Fig. 115),

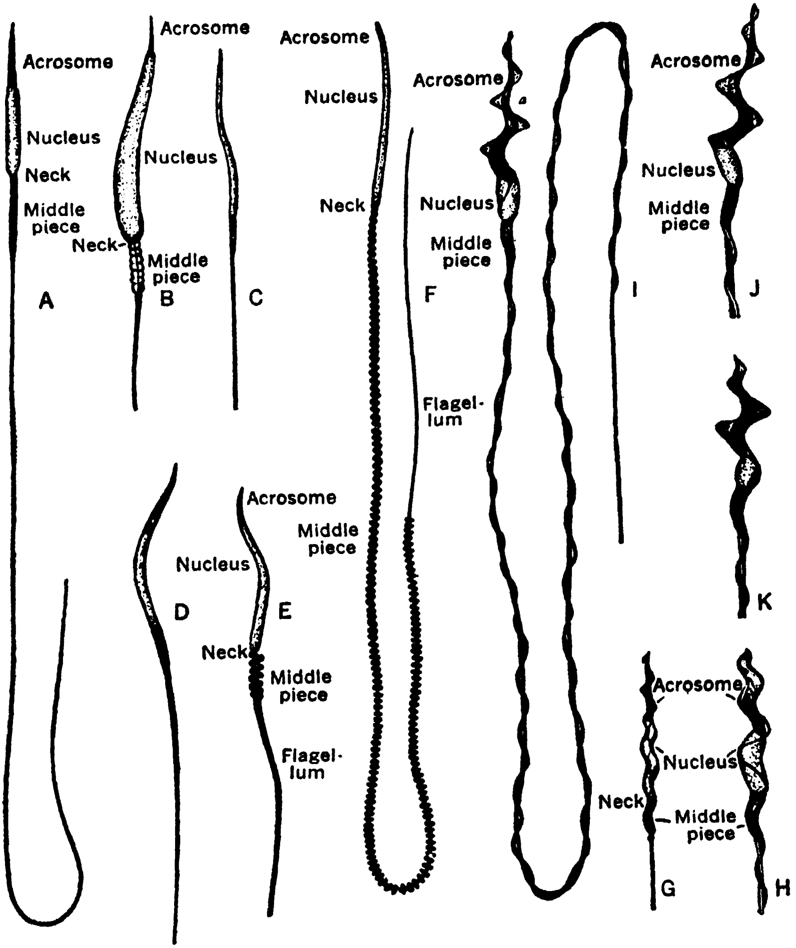


Fig. 112. Sperms of various reptiles and birds. A, chameleon; B, a turtle; D, E, the fowl *Gallus;* F, the pigeon; G, H, I, J, K, various other birds. (From Wilson, *The Cell in Development and Heredity*, after Retzius, by permission of The Macmillan Company, publishers.)

for example, the cytoplasm and nucleus are concentrated in the form of a small disc, the blastoderm, at one side, the remainder of the relatively large cell being filled with yolk.

The vertebrate egg is usually surrounded by various protective envelopes. These may be divided into three kinds depending on the place and manner of their formation. Those derived from the egg itself are known as primary membranes. The delicate vitelline membrane is an example of this type. Secondary envelopes are formed by the follicle cells which immediately surround the egg. An example of this type is the "chorion" of the hagfish, *Myxine*. The membranes or shells which are added to the egg during its passage through the oviduct are known as tertiary envelopes. Among the many examples of this type are the albumen, shell membranes, and the shells of the reptilian and avian egg; the horny capsules of the elasmobranch egg and the jellylike covering of the eggs of many amphibians and bony fishes. Most tertiary membranes are not formed until after fertilization.

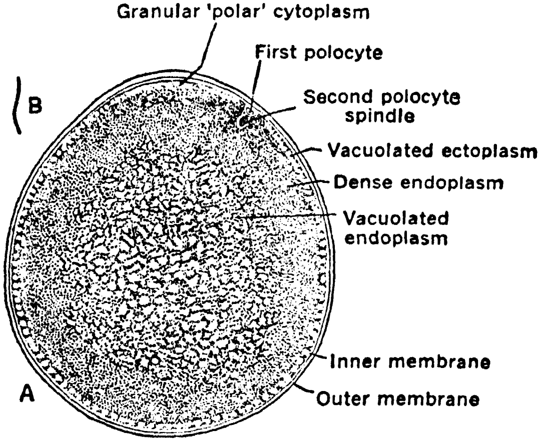


Fig. 113. A, section through the egg of a primitive vertebrate, the lamprey; B, sperm of the same species drawn to scale. (From Woodruff, *Animal Biology*, after Herfort, by permission of The Macmillan Company, publishers.

The arrangement of yolk and cytoplasm gives to the egg a definite symmetry. A line drawn from the center of the cytoplasmic mass to the center of the yolk passes through the center of the egg. Such a line is known as the egg axis, and its ends as the animal and vegetal poles. The animal pole may be identified by the presence of the polar bodies and the vegetal pole by the greater concentration of yolk in that half of the egg. The nucleus is located in the egg axis and nearer to the animal pole. It contains one or more nucleoli. The arrangement of these structures within the egg has an important relation to the orientation of parts in the development of the embryo.

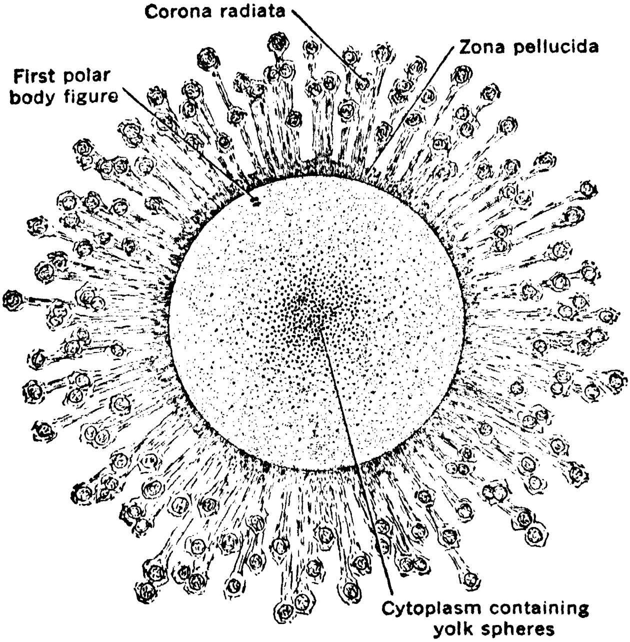


Fig. 114. Human ovum immediately prior to ovulation. The first polar body division figure has been formed. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, after H. Stieve, by permission of The Macmillan Company, publishers.)

FERTILIZATION. The union of the two germ cells is known as fertilization (Fig. 116). Although differing greatly in details in the various vertebrates, the essential features of the process are relatively constant in all of them. The motile sperm approaches the ovum and upon making contact with it, the movement of the flagellum ceases. The entrance is usually near the animal pole. The sperm seems to be drawn in by the action of the cytoplasm of the egg. In some forms the tail enters the egg, while in others it is broken off and left outside. In either case, it plays no further part in the formation of the embryo. In a number of forms the spermatozoon enters by way of an opening in the egg membranes. This is the micropyle. As soon as the head of the spermatozoon enters the cytoplasm of the ovum, a number of remarkable changes take place. A cone-shaped plug of albuminous material is concentrated around the acrosome. The apex of this body, which is known as the entrance funnel, is directed toward the center of the ovum. The entrance funnel enlarges, the apex penetrating deeper into the interior of the ovum and carrying with it the spermatozoon. During this movement toward the axis of the egg, the male germ cell is rotated through an angle of 180° so that the acrosome is pointing toward the periphery of the egg, and the anterior centrosome toward its center. A clear area now appears around the centrosome. This is known as the sperm-sphere. From this sphere radial fibers pass out in all directions, form-

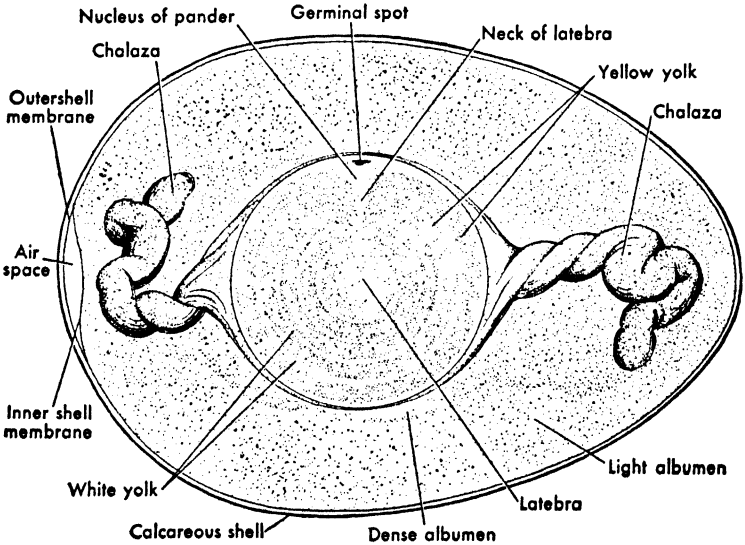


Fig. 115. The chick egg and its membranes. (Adapted from Thompson, redrawn from Huettner, *Fundamentals of Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

ing the sperm aster. The centrosome then disappears, and, as the tail also has degenerated, the subsequent changes involve the sperm nucleus only. This shortens, thickens, and becomes

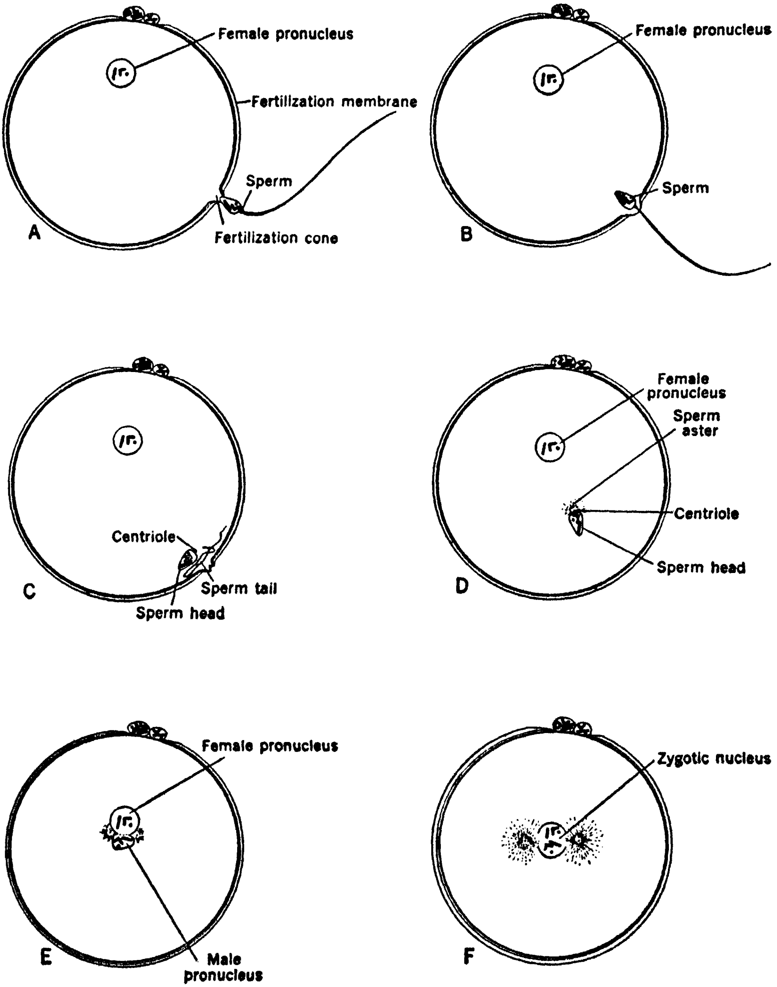


Fig. 116. Scheme of fertilization of the ovum. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

highly vacuolated until it resembles in appearance an ordinary nucleus. It is known as the male pronucleus, and it lies outside the sperm aster. The nuclear membrane on the side facing the sperm aster is ruptured, and a round granular body, the definitive centrosome, leaves the nucleus.

In the meantime, the female pronucleus has left its former position near the animal pole and moved toward the center of the ovum. The centrosome and aster, followed by the male pronucleus, now advance to meet the female pronucleus. During this movement, the centrosome divides. The daughter centrosomes thus formed take up such a position that the two pronuclei meet between them. Fine fibers now pass from both centrosomes, forming a fertilization spindle as well as new asters. Both pronuclei enlarge, and the chromosomes take form within them. The chromosome number of each is that previously mentioned as characteristic of the germ cells following the maturation division, or, in other words, one half that of the somatic cells of the same species. The maternal and paternal chromosomes now line up on the equator of the fertilization spindle. They next divide by a longitudinal division as in ordinary mitosis. The daughter chromosomes thus formed pass to the poles of the spindle to enter into the formation of the daughter nuclei. It will be seen that these nuclei, when formed, will contain a full set of maternal and also of paternal chromosomes. The subsequent division of the cytoplasm will result in the formation of two daughter cells, each of which will contain the somatic number of chromosomes. This number will be constant in all subsequent divisions of each somatic cell in the body.

SEGMENTATION. The divisions of the ovum which follow fertilization constitute segmentation, or cleavage (Fig. 117). A series of cell divisions takes place resulting in a two-cell, then a four-cell, then an eight-cell stage, and so on, until a small body is formed composed of numerous cells which are relatively equal in size. These cells are known as blastomeres. The details of the later divisions vary greatly in the different vertebrate groups, being largely influenced by the amount of yolk present in the egg (Fig. 118). As a result of these early divisions in the lower vertebrates, a hollow, more or less spherical mass of cells is formed (Fig. 119). This is

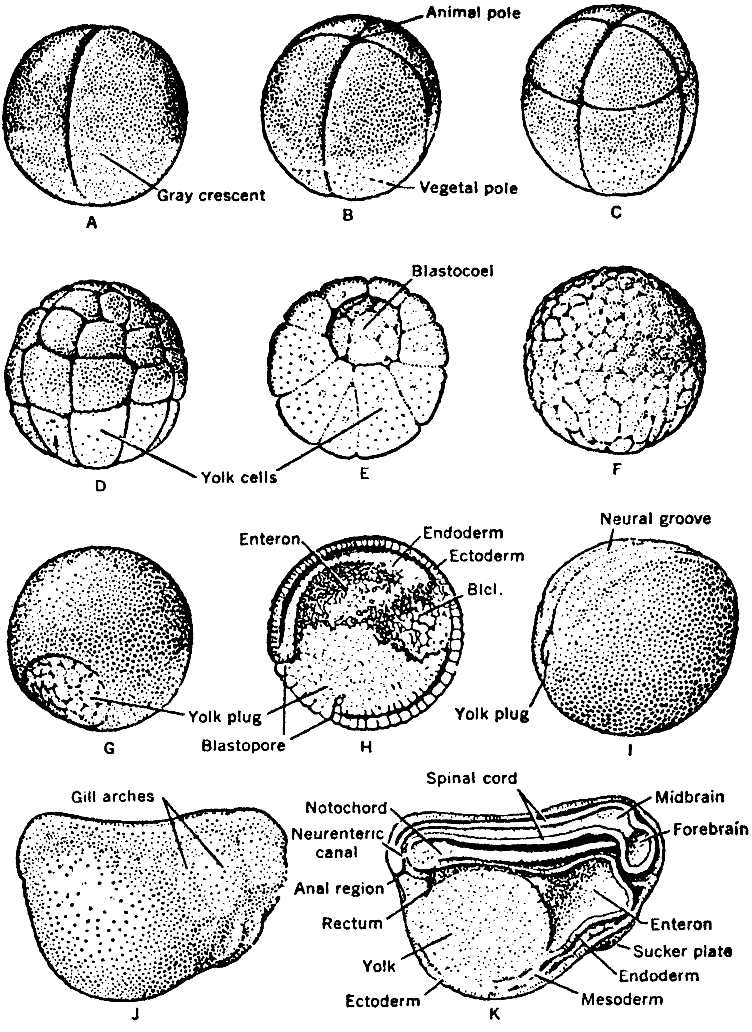


Fig. 117. Early development of the frog. A, B, C, egg at two-, four-, and eight-cell stages; D, early blastula; E, section of D; F, late blastula; G, early gastrula: overgrowth of ectoderm (cells of ectoderm now too small to be shown in figure); H, section of G showing germ layers, etc. (*Blcl*, blastocoel); I, late gastrula: formation of neural groove and folds representing the foundations of the nervous system; J, older embryo, with neural groove closed, assuming tadpole form; K, section of J. (From Woodruff, *Foundations of Biology*, by permission of The Macmillan Company, publishers.)

called the blastula, and the cavity within, the blastocoel or segmentation cavity. In some cases as in *Amphioxus* the blastocoel is a spherical cavity surrounded by a single layer of cells, the blastoderm, which are relatively equal in size and shape.

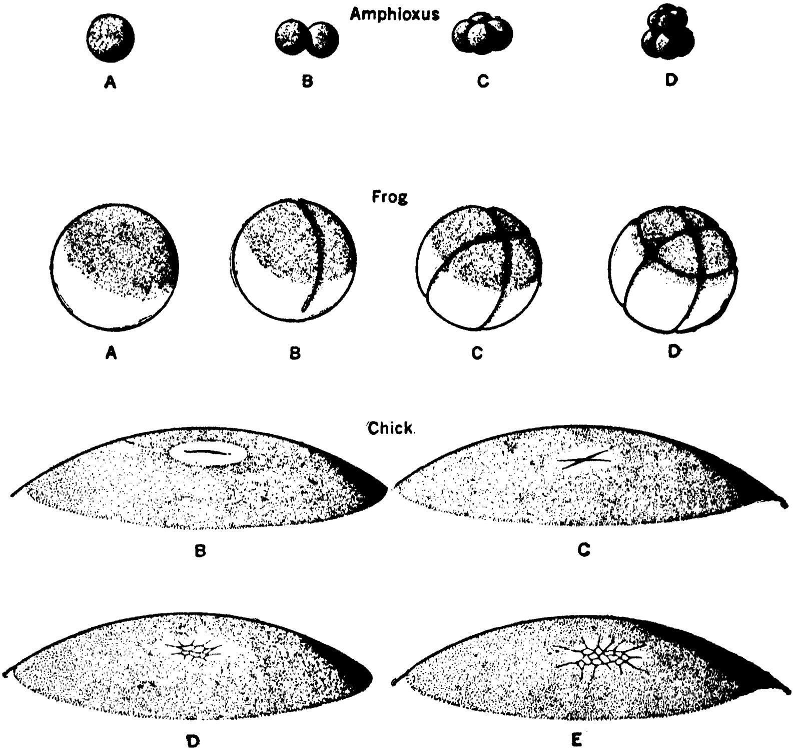


Fig. 118. Comparative cleavage of three types of eggs. The letters from A to D refer to identical stages. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

In the frog the blastula, while still spherical in shape, is quite different internally due to the greater amount of yolk present (Fig. 120B). The blastoderm is made up of several layers of cells due to the fact that there are tangential as well as horizontal and vertical divisions. The cells at the animal pole (micromeres) are much smaller than those at the vegetal pole (macromeres).

In an extremely telolecithal egg, like that of birds, the cleavage plane does not pass through the yolk. As a result, the blastula consists of a disc-shaped group of cells (blastodisc) separated from the undivided yolk by a shallow blastocoel (Fig. 120C).

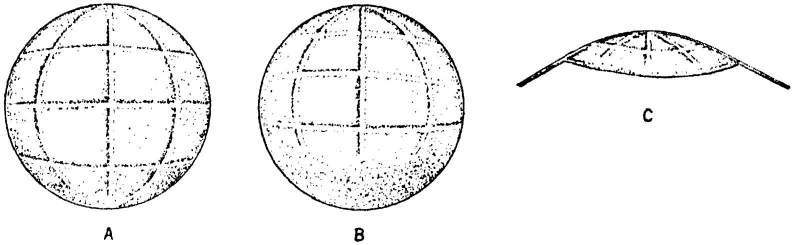


Fig. 119. Diagram to show main types of cleavage in vertebrates. A, equal holoblastic; B, unequal holoblastic; C, meroblastic. (Reprinted by permission from *Introduction to Vertebrate Embryology*, fourth edition, by W. Shumway, published by John Wiley & Sons, Inc.)

In mammals, after the first few divisions, cleavage becomes irregular and, as it takes place in various planes, a solid mass of unequal cells is formed. This is known as the morula. Later a blastocoel appears, apparently due to accumulation of fluid in the morula (Fig. 120D). This cavity is irregular in shape and eccentrically placed. The thick body of cells on one side of the cavity is the embryonic disc, while the single layer surrounding the rest of the cavity is the trophoblast.

THE GASTRULA AND THE GERM LAYERS. Later, through the movement of cells from the exterior to the interior, the blastula becomes converted into an embryo of two germ layers, known as a gastrula. The simplest type of gastrulation is illustrated in *Amphioxus*. The process involved is largely an invagination of the more columnar cells of the vegetal hemisphere. As a result of this inpushing of cells a cuplike group of cells is formed. The wall of the cup consists of two layers of cells, an outer ectoderm and an inner endoderm. These are the so-called primary germ layers, and from them all the tissues and organs of the body are subsequently formed. The new cavity, which is immediately surrounded by endoderm, is the gastrocoel or archenteron. The opening into it is known as the blastopore. With the deepening of the cavity of the gastrula, the old blastocoel is eventually obliterated.

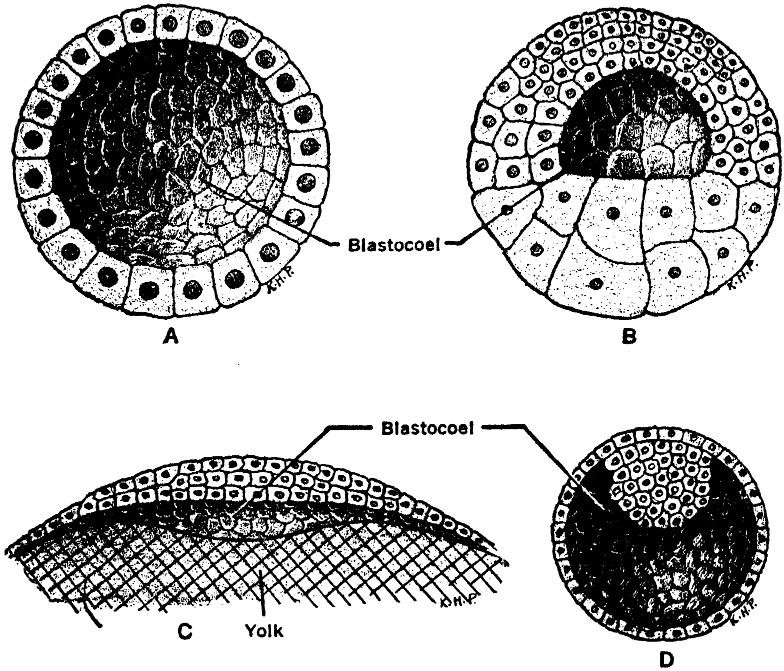


Fig. 120. Diagrams of vertebrate blastulae. A, coeloblastula following holoblastic equal cleavage (*Amphioxus*); B, coeloblastula following holoblastic unequal cleavage (frog); C, discoblastula following meroblastic cleavage (chick); D, blastocyst (mammals). (Reprinted by permission from *Introduction to Vertebrate Embryology*, fourth edition, by W. Shumway, published by John Wiley & Sons, Inc.)

In the vertebrates (Fig. 117H) the formation of the gastrula is a much more complicated process than in the form described. Various types of cell movements, such as involution, epiboly, and concrescence have been described. For a discussion of these various types of gastrulation, the student is referred to any modern text on Vertebrate Embryology.

FORMATION OF MESODERM. The third germ layer or mesoderm is derived from cells which were temporarily associated with both ectoderm and endoderm. This middle layer when first seen as separate from endoderm and ectoderm (Fig. 5), consists of the notochord in the center and a sheet of mesoderm on each side. Because of this relationship between the notochord and mesoderm, this middle layer of cells is often referred to in embryology texts as the chordamesoderm.

There is much difference in detail in the manner in which mesoderm is formed in different vertebrates. In *Amphioxus* (Fig. 2), hollow pouches grow out from the dorsolateral regions of the endoderm. These eventually become cut off from the endoderm and grow laterally and ventrally to fill the space between ectoderm and endoderm. Because of their manner of formation, each segment of mesoderm has a cavity which is a coelom. The wall of the cavity just inside the ectoderm is known as somatic mesoderm; that just outside the endoderm, as the splanchnic mesoderm. The solid strip of cells in the middorsal roof of the archenteron between the mesodermal pouches becomes the notochord.

In the vertebrates the mesoderm is not segmented at first, but appears in the form of paired sheets which extend laterally and ventrally (Fig. 6). These sheets later become divided into somatic and splanchnic layers by the appearance of a split between them. This split is the beginning of the coelom.

THE NERVE CORD. At a relatively early period in the development of the embryo, the ectodermal cells along the middorsal region multiply more rapidly than the others. This results in the formation of a thickened plate of cells, the neural, or medullary plate (Fig. 121). By the continuation of this unequal growth, the edges of this plate are raised and a groove is formed between them. This is the medullary groove. Later the edges of the groove meet dorsally in the median line, forming a tube. The tube thus formed separates from the ectoderm from which it was derived. This is the neural tube and the process by which it was formed is called invagination. The anterior end eventually gives rise to the brain, while the rest of the tube remains as the tubular nerve cord characteristic of the chordates.

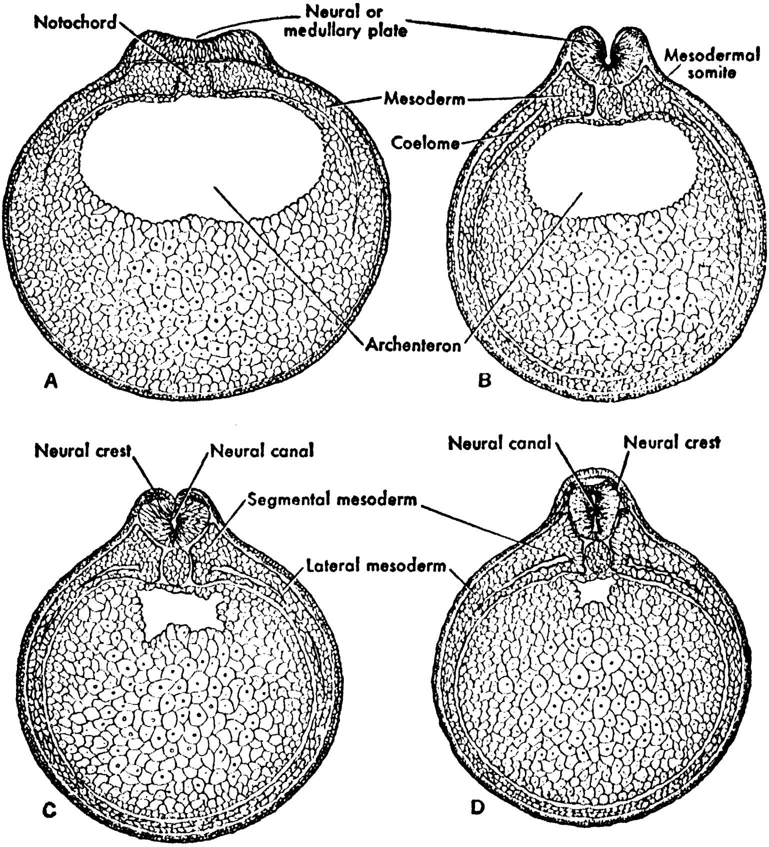


Fig. 121. Formation of the neural tube from the neural plate. A, neural plate, 2.00 mm. embryo; B, neural folds, 2.25 mm. embryo; C, neural folds fusing, 2.35 mm. embryo; D, neural tube completed, 2.60 mm. embryo. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

THE NOTOCHORD. As described above, the notochord in *Amphioxus* develops from the median strip of endoderm between the mesodermal pouches (Fig. 2). In the vertebrates the development of this important structure is apparently much less simple, for there is much disagreement concerning the manner of its origin. Without discussing the merits of these different opinions, it can be stated that the notochord appears early as a solid rod of cells separate from the three germ layers which may have contributed to its formation. It lies in the middorsal region between the nerve cord and the alimentary canal. It later becomes surrounded by sheaths of mesenchymal origin which are important in connection with the development of parts of the skeleton.

THE ALIMENTARY CANAL. After the formation of the notochord and the mesoderm, the endoderm remains surrounding the tubular cavity, or archenteron. This tube is always closed at the anterior end and usually at the posterior end. An invagination of the ectoderm near the anterior end results in the formation of a pocket which is pushed in to meet the cavity of the tube. This is the stomodaeum (Fig. 252). The intervening layers of cells eventually break through, and the mouth cavity leading into the alimentary canal is formed. In a similar manner, the proctodaeum is formed at the posterior end. This eventually connects with the canal forming a posterior opening, the anus.

MESODERMAL SOMITES. It was stated previously, in connection with the discussion of the characteristics of vertebrates, that many of the body structures are segmented, or metameric. This repetition of similar parts is first seen in the development of the mesoderm and of the structures derived from it. The mesodermal pouches, or lateral sheets as described above, were located dorsal to the archenteron, or primitive alimentary canal, and lateral to the notochord. They are now extended ventrally to surround the archenteron almost completely and dorsally to lie at the sides of the notochord and nerve cord (Fig. 7). These enlarged areas of mesoderm enclosing the two body cavities may be quite definitely divided horizontally into three distinct regions, a dorsal epimere, a ventral hypomere, and an intermediate mesomere. A series of constrictions next extends vertically downward through the epimere. This results in the formation of a series of fingerlike cavities in these regions, all of which are connected with the common cavity of the mesomere and hypomere. The epimeres are later separated from the other two portions, and, as a result, a series of paired cubes are formed.

The epimeres give rise laterally to groups of mesenchyme cells, the dermatomes. From these the inner layer of the skin, or dermis, is later developed. The medial wall of each epimere also gives rise to mesenchyme cells, the sclerotomes, which later contribute to the formation of the skeleton. The remaining portion of the epimeres, the myotomes, remain and give rise to muscle segments or myomeres, which are later separated from one another by partitions of connective tissue, the myosepta. The myotomes of the two sides grow down (Fig. 122) between ectoderm and the hypomere to meet in the median ventral line. They give rise to the voluntary muscles of the body.

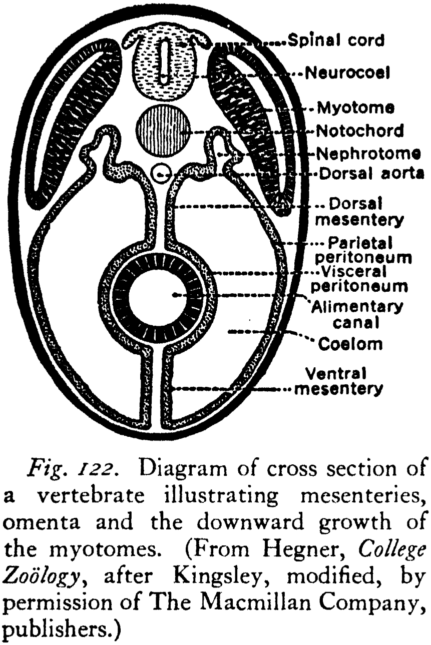


Fig. 122. Diagram of cross section of a vertebrate illustrating mesenteries, omenta and the downward growth of the myotomes. (From Hegner, *College Zoölogy*, after Kingsley, modified, by permission of The Macmillan Company, publishers.)

The middle region, or mesomere, later gives rise to the excretory system, to the reproductive organs, and to the ducts of both systems. The portions which form the excretory structures are known as nephrotomes. The mesomere is not segmented.

The remaining third of the original regions of mesoderm, the hypomere, is also not divided into segments by vertical constrictions. The cavity within is known as a metacoel, or coelom. The hypomeres of the two sides increase in extent until they meet dorsal and ventral to the alimentary canal. The double membranes thus formed are the dorsal and ventral mesenteries respectively. That portion of the wall of the coelom between these two mesenteries is closely applied to the parts of the alimentary canal. It is known as the splanchnic or visceral, peritoneum. The opposite wall, lying just within the body muscles, is the somatic or parietal, peritoneum. The ventral mesentery eventually almost completely disappears, as a result of which the two metacoels communicate with one another to form the body cavity characteristic of the adult. The dorsal mesentery remains, aiding in the support of the alimentary canal and forming a bridge over which pass blood vessels, nerves, etc. As the various organs of digestion are differentiated from the primitive alimentary canal, they come to be supported by similar double membranes formed from the splanchnic peritoneum. These are known as omenta.

The smooth muscles and connective tissue layers of the alimentary canal and of all of its derivatives are formed from mesenchyme originating in the splanchnic walls of the hypomere. In the anterior part of the body this region gives rise to the heart and to some of the voluntary muscles (branchiomeric).

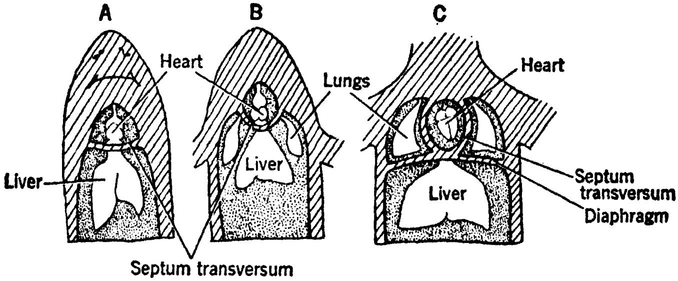


Fig. 123. Diagrams showing the relations of the coelomic cavities (stippled). A, fishes; B, amphibians, reptiles and birds; C, mammals. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

The body cavity is later divided by the septum transversum into an anterior cavity, the pericardial, containing the heart; and a posterior chamber, the pleuroperitoneal cavity, which contains the remaining viscera (Fig. 123). In the mammals, a second transverse partition, the diaphragm, appears. This is connected to the central portion of the septum transversum in such a way that two small anterior cavities, the pleural, are separated from the posterior part, which is now called the peritoneal (abdominal) cavity. The entire cavity anterior to the diaphragm is also known as the thoracic cavity. The pleural cavities, each containing a lung, are lined with a thin membrane known as the pleura. This, like the peritoneum of the abdominal cavity, consists of both somatic and splanchnic regions. The somatic pleura of the two cavities forms a double membrane between them, medially and ventrally. This is known as the mediastinal septum. The space between the two layers of the septum is the mediastinum. Dorsal to the septum the cavity is largely filled by the heart, which is surrounded by its own covering membrane, the pericardium.

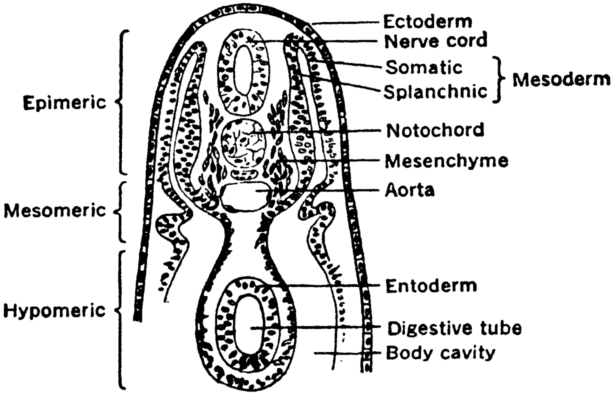


Fig. 124. Diagram of cross section of dogfish, showing migration of mesenchyme. (From Walter, *Biology of the Vertebrates*, after Van Wijhe, by permission of The Macmillan Company, publishers.)

THE MESENCHYME. The formation of mesenchyme was referred to above in connection with the origin of sclerotomes and dermatomes. Mesenchyme is derived very largely from mesoderm but may come also from the other germ layers. It is a tissue consisting of branching, irregularly shaped cells which are somewhat united with one another to form a network. The cells are amoebic in character, wander-ing from their places of origin into various spaces of the body where they give rise to many structures (Fig. 124). Among these may be mentioned connective tissue, cartilage and bone, the smooth muscles of the viscera, the blood corpuscles, and the blood and lymph vessels.

SUMMARY

The vertebrate body is formed as the result of a series of cell divisions of a fertilized egg, or zygote. Before fertilization, the germ cells, egg and sperm, are prepared by a process of maturation. As a result of these preparatory changes, from each primordial germ cell there are produced, in the male, four mature spermatozoa, and in the female, one mature ovum. In both sexes, the developed germ cells contain the chromosome content characteristic of the species, that is, one half the number present in other cells of the individual animal.

The sperm cell is typically smaller than the ovum, it is flagellated and contains little cytoplasm. The ovum is a relatively large cell, more or less spherical in shape, and containing varying amounts of yolk.

The union of the sperm cell and the egg is known as fertilization. During this process the sperm cell penetrates the egg; chromosomes form within the nucleus of each germ cell; the chromosomes take their position at the equator of the fertilization spindle; they divide longitudinally as in ordinary mitosis; half the chromosomes pass to the poles of the spindle and take part in the formation of daughter nuclei; the cytoplasm subsequently divides, giving two cells each containing the somatic number of chromosomes.

This division and those which follow constitute segmentation or cleavage. A solid body of cells is formed first. This later takes the form of a hollow sphere of cells known as the blastula. One side of this later invaginates forming a cuplike group of cells, the gastrula. The outer layer of cells is the ectoderm, the inner the endoderm. Between these primary germ layers a third layer later develops. This is the mesoderm.

From the ectodermal cells along the middorsal region, the nerve cord forms by a process of invagination.

The endoderm remains as the lining of the alimentary canal, which represents the original archenteron.

The developing mesoderm is in the form of segments which become partially divided into three regions, an epimere, a mesomere, and a hypomere. The dorsal region (epimere) contributes to the formation of dermis, the muscles, and the skeleton. The middle region (mesomere) gives rise to the excretory and reproductive systems. The ventral region (hypomere) gives rise to mesenteries, omenta, the linings of the coelom, the smooth muscles of the viscera, and, in the anterior region, to some of the voluntary muscles.

VI. The Integument

The vertebrate integument, or skin, consists of the outer covering of the body with its various layers of tissue, together with the numerous structures which are derived as a result of the activity of the cells of these tissues. It may be considered to be a definite organ having a double origin and performing many important functions. In general, the skin of vertebrates consists of two definite regions, each made up of several layers of cells. The outer of these, the epidermis, is ectodermal, while the inner, or dermis, is mesodermal. A variety of structures such as glands, scales, claws, feathers, hair, etc., are derived from these layers. Some of these structures are formed from the outer layer of the skin, others from the inner layer, while, in the formation of some, both regions play a part.

HISTOLOGY

It should be recalled that the skin of a non-chordate, such as the earthworm, consists of a single layer of epithelial cells known as the hypodermis. External to this is a thin noncellular layer, the cuticle, which is secreted by the hypodermal cells. Just below the hypodermis are the muscles of the body wall. The epithelial cells of the hypodermis may be flat as in the sponges and the coelenterates, columnar (Fig. 125) or cuboidal as in the annelid worms, or ciliated as in some flatworms. Some of the epithelial cells may be differentiated to form simple sensory or glandular cells. In some non-chordates, a chitinous or calcareous exoskeleton is secreted by the cells of the hypodermis.

In *Amphioxus* (Fig. 126) the integument is essentially of the vertebrate type in that it is composed of more than one layer of tissue. The outer layer, or epidermis, consists of a single layer of columnar epithelium resembling the hypodermis of the annelid worm. These cells are ciliated in the larval stage, but in the adult are covered with a thin non-cellular cuticle. Beneath the epidermis is a thin layer of connective tissue, the dermis, or corium, covering the body muscles.

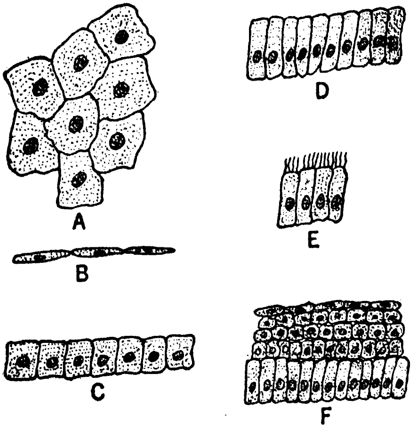


Fig. 125. Types of epithelial cells. A, squamous, surface view; B, the same, sectioned; C, cuboidal; D, columnar: E, ciliated columnar; F, stratified.

In the vertebrates (Fig. 127) the epidermis differs from that of the forms just described in being composed of several layers of cells. The innermost of these is known as the stratum germinativum, or the Malpighian layer. As the former name implies, this is a layer of actively multiplying cells, which give rise to the remainder of the epidermis as well as to many accessory structures. The new cells formed by the division of the cells of this layer are constantly being forced outward to the exposed surface of the integument. During this migration, the structure of the cells is greatly modified. They are flattened out, the membranes are thickened, the nuclei break up, and eventually only dead remnants remain. This outer layer of dead tissue is known as the stratum corneum and is composed largely of a material called keratin. The thickness of the corneal layer varies greatly in different vertebrates, as well as in different regions of the body of any individual species. This outer layer must be constantly removed in order to prevent its excessive increase in thickness. In the amphibia and reptiles the entire outer layer is

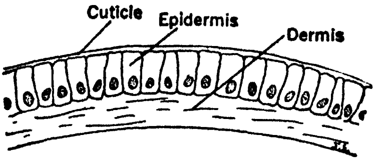


Fig. 126. Section of the skin of *Amphioxus.*

shed periodically by a process of moulting, or ecdysis. In birds and mammals there is no general moulting of the skin, but the dead remnants are being constantly and unnoticeably worn away.

It is possible to distinguish two more or less clearly defined transitional layers between the stratum corneum and the Malpighian layer. The outer of these is termed the stratum lucidum: the inner, the stratum granulosum.

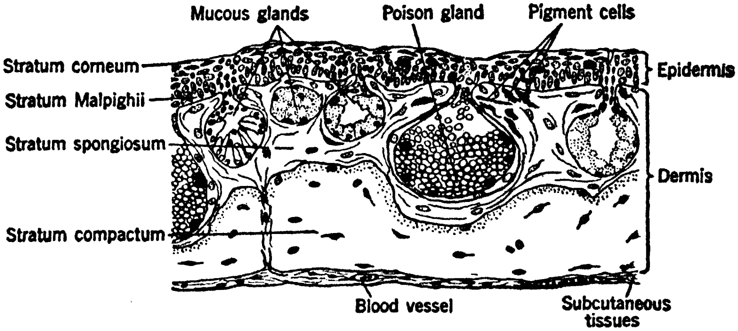


Fig. 127. Section of frog skin showing histology. (Drawn by Sarah W. Eyre.)

With the exception of the accessory bodies derived from it, the epidermis contains little in the way of associated structures. Sensory nerve endings of a simple nature are quite freely distributed among its cells. Pigment cells are often found in the Malpighian layer. They sometimes originate in this region, but more often wander in from their place of origin in the deeper layers. Blood vessels are almost never found in the epidermis. The cells of the Malpighian layer must, therefore, be nourished by capillaries located in the dermis.

The second region of the skin of vertebrates is known as the dermis, or corium. It is made up largely of connective tissue and is usually much thicker than the epidermis. It has the appearance of a confusing network of cells and of fibers which extend among the cells in all directions. It is this layer of the skin of mammals from which leather is made. Beneath the corium is a subcutaneous layer connecting the skin rather loosely with the underlying muscles. In contrast with the epidermis the dermis contains a variety of structures such as blood and lymph vessels, nerve endings, simple sense organs, pigment cells, deposits of fat, and smooth muscle cells.

DERIVATIVES OF THE INTEGUMENT

It was previously stated that both parts of the integument give rise to a variety of characteristic structures and also that they collaborate in the formation of others. The mere presence of a certain structure in either region is no proof that it originated there. Many bodies which arise in the epidermis, for example, hair and glands, dip down into the dermis for greater protection, as well as for establishing relations with the circulatory and nervous systems. In the pages which immediately follow, a description of the integumental structures characteristic of the different vertebrate classes will be given.

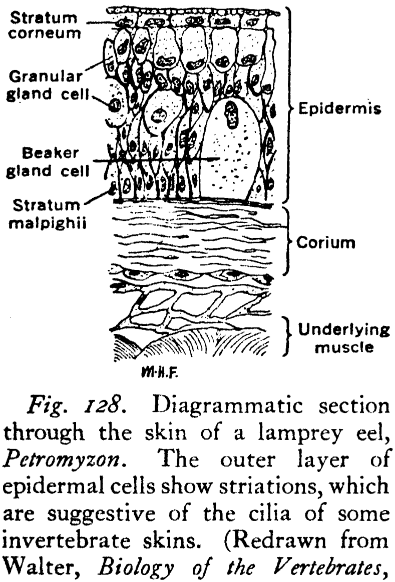


Fig. 128. Diagrammatic section through the skin of a lamprey eel, *Petromyzon*. The outer layer of epidermal cells show striations, which are suggestive of the cilia of some invertebrate skins. (Redrawn from Walter, *Biology of the Vertebrates*, after Haller, by permission of The Macmillan Company, publishers.)

CYCLOSTOMES. The most distinctive feature of the integument in the cyclostomes (Fig. 128) is the presence of numerous glands. A gland may be defined as a cellular structure which produces a secretion or an excretion. The glands present in the skin of the cyclostomes are of the simplest possible type, being merely single epidermal cells differing from their neighbors in being specialized for the production of a secretion. As seen here, they are of two types, namely, granular cells and the so-called "beaker cells." The latter are much enlarged elliptical cells which often extend through the whole thickness of the epidermis. The mucus secretion of these numerous glands serves to make the surface of the body slippery and possibly is an aid to locomotion in water.

The horny teeth (Fig. 129) of *Petromyzon* and other related forms are corneal modifications of the epidermis. These pointed teeth, arranged in regular rows around the circular mouth, are periodically shed and subsequently renewed. In other regions of the body, there is no definite corneal layer, the outer cells having formed a cuticle resembling that of the non-chordates.

The corium is thinner than the epidermis in the members of this class, and gives rise to no important structures.

FISHES. In the integument of fishes also, the epidermis is highly glandular. Many of these glands are simple and one-celled, similar to those present in the cyclostomes. These unicellular glands produce a mucus or slime, the primary function of which is to protect the surface from the action of water and from parasites. In the African lungfish, *Protopterus*, certain glands produce a cocoon in which the animal remains while buried in the mud during the dry season. In certain selachians, the male is provided with pterygopodial glands associated with the claspers and evidently concerned with copulation. Many deep-sea forms are provided with highly modified integumental glands that produce luminescence.

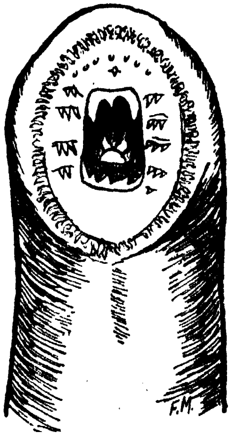


Fig. 129. Head of cyclostome, *Entosphenus tridentatus*, showing horny "teeth."

The most distinctive structures arising in the integument of fishes are the scales. Although some fishes, like the eels, have a smooth skin, this is evidently a secondary modification, since scales are present in the embryo. At least four types of scales may be distinguished in these classes, namely, placoid, ganoid, cycloid, and ctenoid.

The placoid scales (Fig. 130), which are the most primitive of these types, are found in a majority of the elasmobranchs.

This kind of scale consists of a flattened base embedded in the skin with a pointed or rounded spine projecting from it. It has been taught for many years that the hard outer surface of the spine of a placoid scale consists of enamel. Recent evidence seems to contradict this and to show that it is merely a harder kind of dentine. During the development of the scale a dermal papilla pushes up, in the form of a cone, beneath the epidermis (Fig. 132). As the dermal papilla comes in contact with the epidermal cells, they become columnar and form an enamel organ resembling the structure present during the development of a vertebrate tooth. The dentine of the scale is secreted by the outer cells of the dermal papilla, while the inner cells remain as the pulp within the pulp cavity. The epidermal cells of the enamel organ later withdraw from around the spine without contributing material to the formation of the scale. It seems, therefore, that the placoid scale is composed entirely of dentine and is of dermal origin. Its embryonic development closely resembles that of the vertebrate tooth. The shape of the scales varies greatly in different species as well as in different parts of the body of the individual. A typical scale of the spiny dogfish consists of a raised median crest terminating posteriorly in a blunt spine, and of two smaller lateral crests. The scales are usually arranged in fairly definite diagonal rows. The rows are separated by

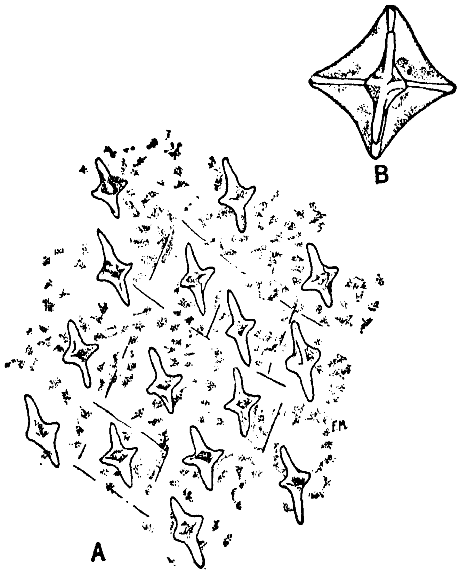


Fig. 130. Placoid scales of *Squalus acanthias.* A, a portion of skin (low-power) showing arrangement; B, one scale (high-power) showing shape.

areas of smooth skin. The similarity existing between these scales and the teeth (Fig. 131), with respect to their structure and origin, has led to a generally accepted belief that they are homologous structures (Fig. 132). Teeth of this character are present in all vertebrate classes above the cyclostomes. They will be discussed at greater length in a subsequent chapter in connection with the digestive system.

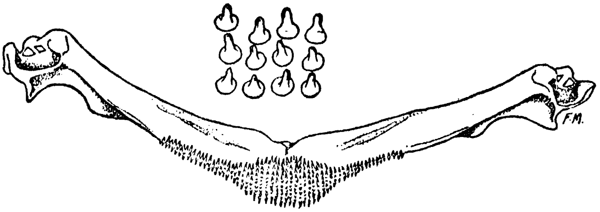


Fig. 131. Lower jaw of skate showing teeth. The small figure shows a few teeth greatly enlarged.

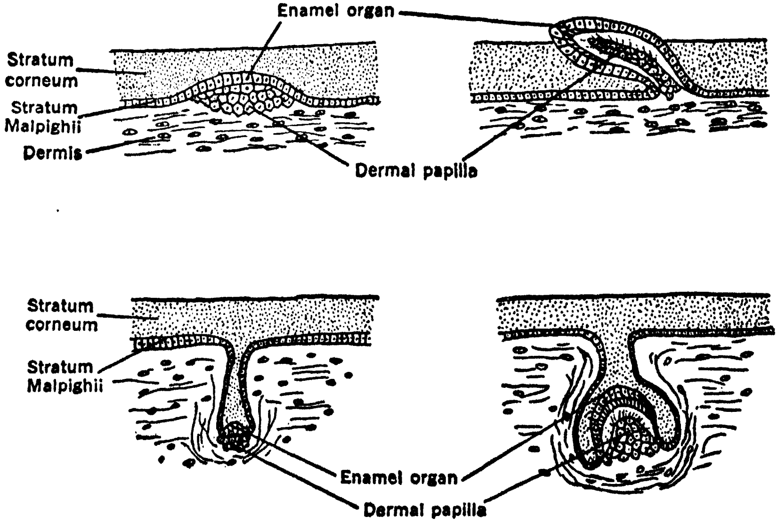


Fig. 132. Diagrams illustrating homology between placoid scales and teeth. Upper figures, a scale. Lower figures, a tooth. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

In many elasmobranchs highly modified scales are found in definite locations. Among these are the heavy fin spines (Fig. 133) of *Squalus acanthias;* the sting of *Dasyatis*, the sting ray; and the heavy teeth on the sides of the long rostrum (Fig. 134) of *Pristis*, the sawfish.

The ganoid scales differ from the preceding type in that the epidermis plays no part in their formation. Composed largely of lamellate bone, the outer surface is covered with a layer of ganoin, a material resembling enamel but derived from the corium. In *Lepidosteus* (Fig. 135), the garpike, and several other related forms, the scales are rhombic in shape and fit closely edge to edge with little overlapping. In these forms, the surface is almost entirely enclosed in a flexible armor formed by these tilelike scales.

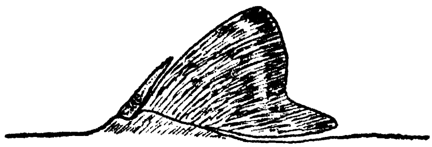


Fig. 133. Dorsal fin of *Squalus acanthias*, showing fin spine.

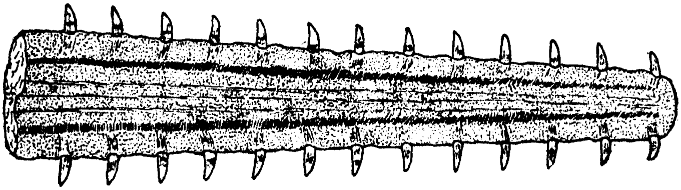


Fig. 134. Saw of *Pristis pectinatus*, the sawfish.

In *Acipenser* and other sturgeons, the scales are larger and much less numerous (Fig. 136), being confined to definite rows along the dorsal margin, the sides of the body, and other of the more exposed regions. These enlarged ganoid scales, or dermal scutes, form a very definite pattern in some regions, particularly in the head (Fig. 137). Many of these remain in the higher vertebrates as the so-called "derm bones" of the skull.

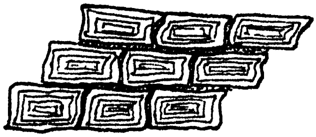


Fig. 135. Ganoid scales of *Lepidosteus osseus*.

Cycloid scales (Fig. 138) resemble the preceding type in being derived from the corium, but differ greatly in shape. Typically, they are roughly circular or ovoid in outline. Under the microscope, a series of lines of growth around a common center are seen. Such scales are arranged in imbricated or overlapping rows like shingles on a roof with the inner margins embedded in the deeper layers of the skin.

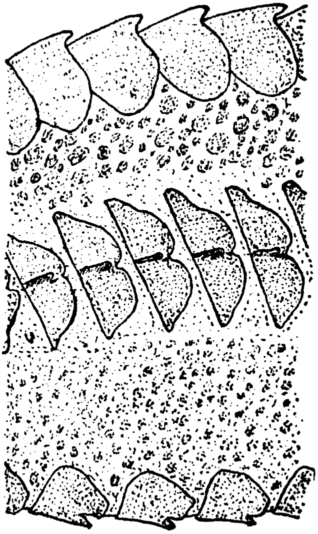


Fig. 136. Ganoid scales of a sturgeon, *Scaphirhynchus platyrhynchus.*

The ctenoid scale (Fig. 139) differs from the cycloid in that the exposed edge bears one or more rows of pointed processes resembling the teeth of a comb. The attached edge is often scalloped and fluted, as a result of which the scales are held more securely in place. A great majority of teleost fishes have either cycloid or ctenoid scales. Both of these types consist of a thin outer bony layer supported by a layer of fibrous connective tissue.

Both regions of the integument show pigment cells (Fig. 140) or chromatophores of various kinds, as a result of which a great variety of color patterns and color changes occur in the fishes. This is especially true in the case of many tropical forms, which are often brilliantly colored.

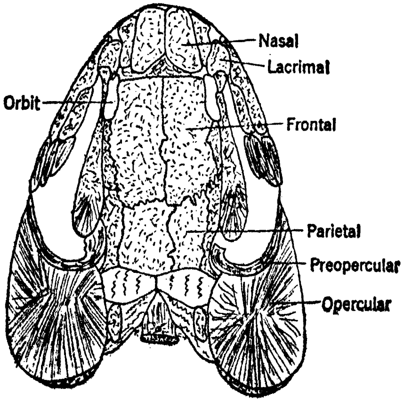


Fig. 137. Skull of *Amia calva*, showing dermal (membrane) bones.

Another type of structure derived from the epidermis is seen in the dogfish. In this, as well as in many other fishes, a series of unjointed horny fin rays, the ceratotrichia, extends beyond the limits of the cartilaginous or bony elements of the fins (Fig. 218).

AMPHIBIANS. The skin of amphibians resembles that of the cyclostomes in many respects. Both regions are relatively thin, although the epidermis consists of several layers of cells. The epidermis gives rise to a large number of glands (Fig. 127). These are more complicated in structure than those previously mentioned in that they consist of many cells instead of a single cell. Such a gland, although arising in the epidermis, eventually pushes deeply into the corium, forming a cavity surrounded by a layer of glandular cells and communicating with the external surface by means of a duct. If a many-celled gland is in the shape of a sphere with a spherical cavity and a relatively narrow duct, it is known as an alveolar gland (Fig. 141). If, on the other hand, the cavity, or lumen, is narrow and has a relatively uniform diameter throughout its length, the gland is said to be of the tubular type. Either of these types of glands may be simple or compound, depending upon whether there is a single glandular body or many such groups of cells whose cavities lead to a common duct.

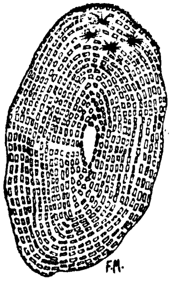


Fig. 138. Cycloid scale from a codfish.

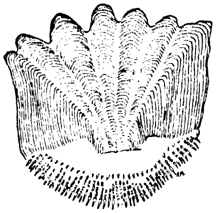


Fig. 139. A ctenoid scale from the perch.

Most of the glands found in the amphibian skin are of the simple alveolar type. Of these there are two main kinds, mucous and poison glands. The former produce a secretion which serves to keep the skin moist, thus contributing to its efficiency as a respiratory organ. The poison glands secrete a mildly poisonous or irritating substance which serves as a means of protection from their many enemies. The digits of tree frogs (Fig. 142)

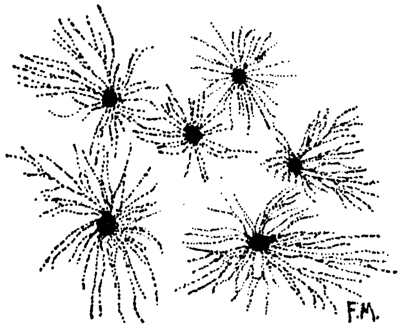


Fig. 140. Pigment cells from a codfish scale.

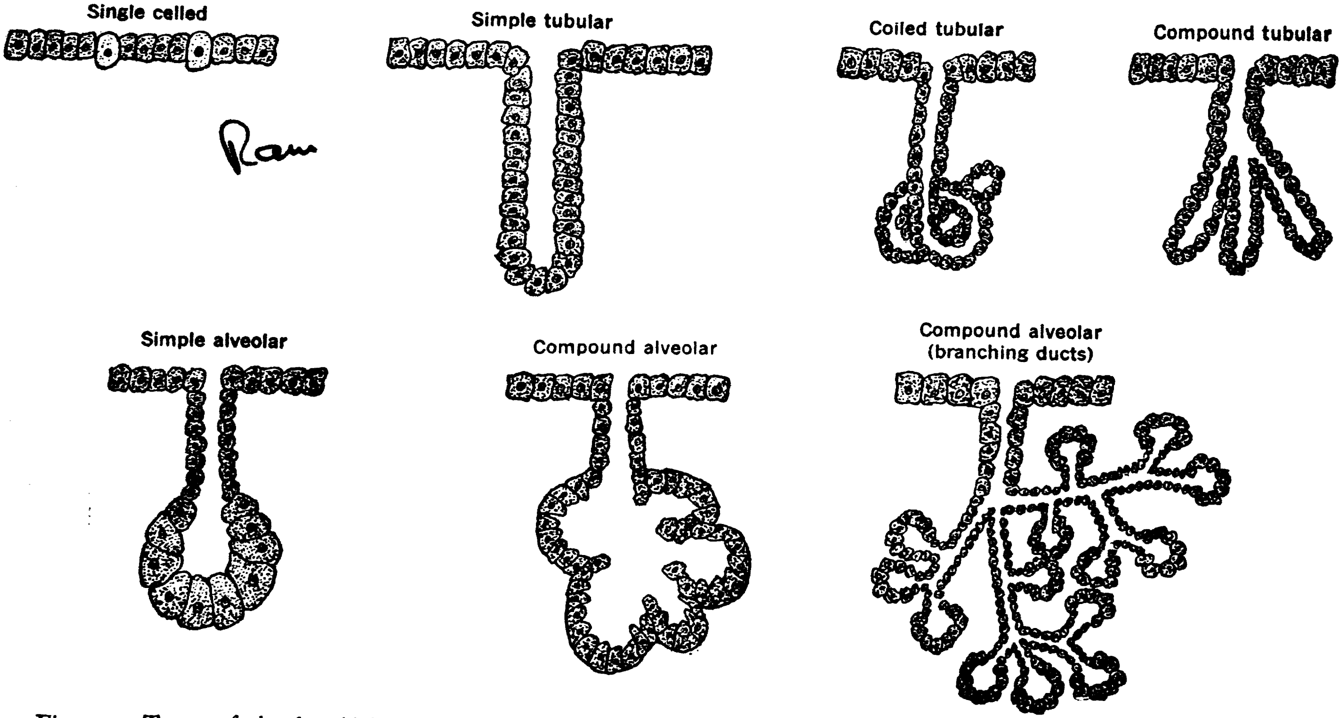


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Fig. 141. Types of glands. (Adapted from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

and certain salamanders are equipped with glandular discs which enable them to cling to the limbs of trees and other similar surfaces.

Among living amphibians, the only evidences of scales in the integument are seen in the order Gymnophiona. In the wormlike caecilians, bands of tiny scales are embedded in the skin.

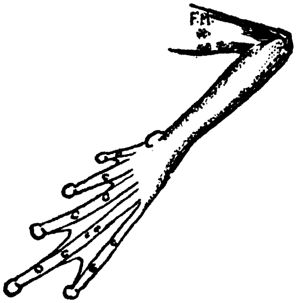


Fig. 142. Hind foot (right), *Hyla versicola*, a tree frog, showing glandular discs.

Finally, the integument of amphibians contains numerous pigment cells. These are usually located in the corium and are said to afford protection to many species, such as the tree toads, by producing coloration resembling that of their environment.

REPTILES. The integument of reptiles is characterized by the general presence of scales, which are entirely epidermal in origin. Vascular papillae in the corium beneath the scales aid in their nourishment, without contributing directly to the formation of the hard parts. In fact, the corium is relatively unimportant throughout the class.

The reptilian scale is composed of horn, or keratin, a material resembling enamel. Such scales serve a double function in these first definitely land-living animals. Many reptiles, as we have seen, are provided with relatively weak organs of locomotion. As a result the body surface is often in contact with the ground, and the thick skin with its numerous scales affords protection against friction. The covering of scales also aids in the prevention of excessive drying of the skin.

The scales of reptiles differ in their arrangement from similar structures in the groups previously considered. In most cases they lie parallel with the surface of the epidermis instead of projecting from it in overlapping rows as in many fishes. In structure and general appearance they occur in almost infinite variety. In the Gila monster (*Heloderma*) the entire surface is covered with rounded scales which, together with the pattern produced by the pigment cells, give the appearance of beautifully colored bead work (Fig. 63). In the turtles the scales are broad and thin scutes overlying a foundation of heavy, bony plates which are of dermal origin (Fig. 52). The outer corneal layer of skin, including the scales, is shed periodically in the reptiles.

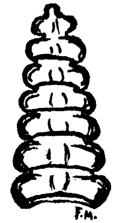


Fig. 143. A rattle from the tail of a rattlesnake.

A variety of other keratin structures appear in the various members of the class. Among these may be mentioned such structures as spines, horns, and claws. Of these three, the claws (Fig. 152) are more generally distributed, not only in the reptiles, but also in the higher vertebrate classes. The claw is a form of digital tip appearing for the first time in this group. It consists typically of two horny plates, the dorsal unguis, and the ventral subunguis. The former is usually convex, curving toward the sides as well as toward the tip, while the latter is flattened or slightly concave and smaller in size. Both plates are derived entirely from the Malpighian layer of the epidermis.

The presence of a horny beak in the turtles should also be mentioned in this connection. This structure, which resembles that so characteristic of the birds, at least partially takes the place of the teeth which have been lost.

The rattle (Fig. 143) at the end of the rattlesnake's tail consists of a series of corneal rings, each of which was left behind at the time of the shedding of the outer layer of epidermis.

The skin of reptiles is practically devoid of glands of any kind. These structures, which were so numerous in the amphibians, are unnecessary in a terrestrial form in which the skin no longer plays a part in respiration. In a few exceptional cases, glands are present in reptiles and these are probably associated with the reproductive function. Among them may be mentioned the scent glands, located around the cloacal opening of many snakes, and crocodilians, and the femoral glands of male lizards, which extend distally from the cloaca along the inner surface of the hind legs.

BIRDS. The skin of the bird is relatively thin and loosely applied to the underlying muscles. The most conspicuous structures in the integument of this group are the feathers. Feathers are derived entirely from the epidermis, and considerable embryological evidence points to their homology to the reptile scale. A feather begins its development (Fig. 144) as a hollow papilla of epidermal cells which dips below the surface. A plug of cells from the dermis fills the cavity of this papilla for a time, but withdraws as the epidermal sheath becomes cornified. On one side of this hollow tube the wall is thickened and this thick portion later forms the shaft of the feather. The opposite portion, which is very thin, eventually splits longitudinally and spreads out flat on either side of the shaft. From these lateral portions the barbs and barbules develop.

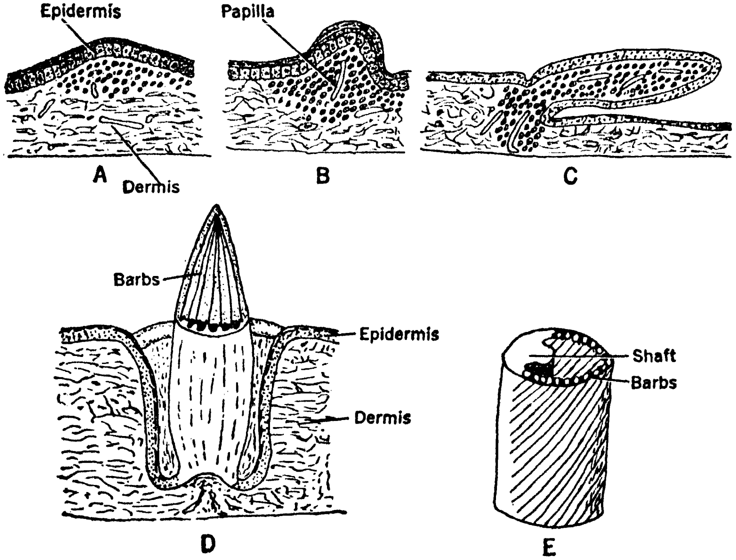


Fig. 144. Diagrams showing the development of a feather. A, B, early stages in formation of papilla; C, early stage of feather; D, later stage of feather and follicle; E, portion of developing feather. (A, B, C, and D, redrawn with modifications from Adams, *An Introduction to the Vertebrates*, by permission of author and publishers, John Wiley and Sons, Inc. E, from Walter, *Biology of the Vertebrates*, after Hesse, by permission of The Macmillan Company, publishers.)

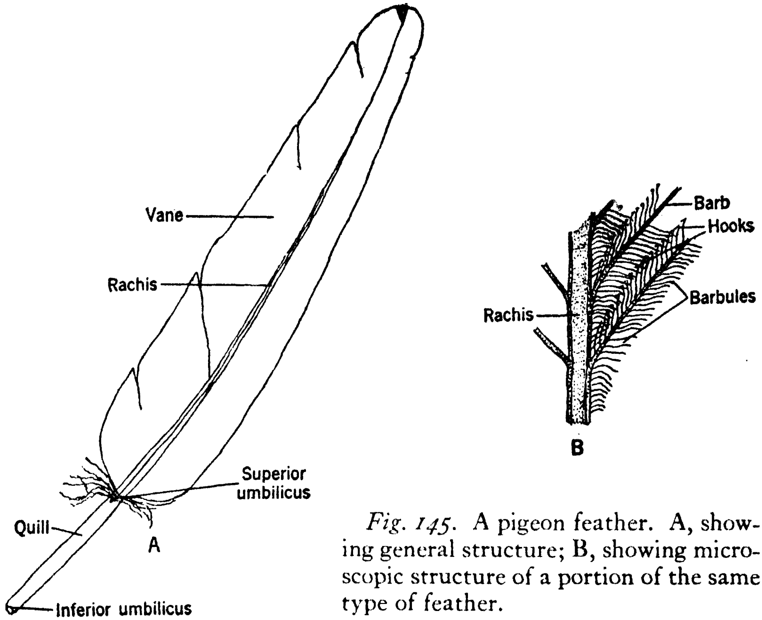


Fig. 145. A pigeon feather. A, showing general structure; B, showing microscopic structure of a portion of the same type of feather.

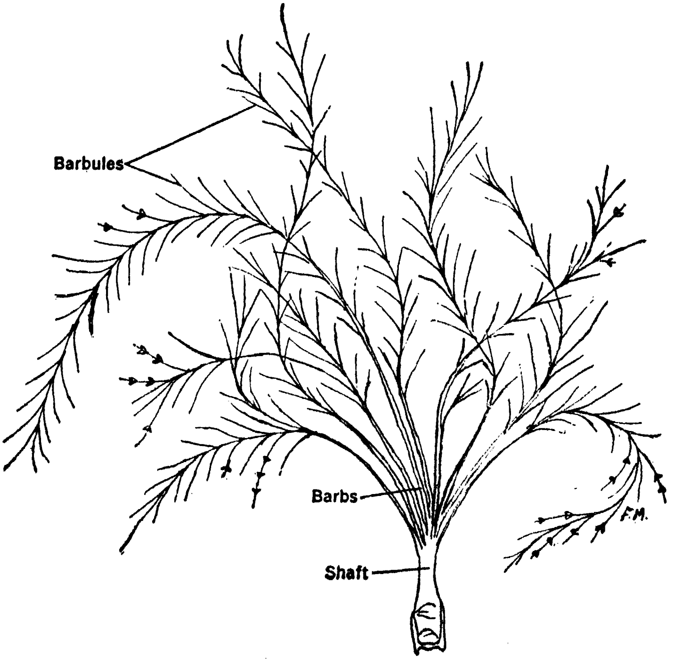


Fig. 146. Down feather. (Details of barbs not completely filled in.)

A typical feather (Fig. 145) consists of the central horny shaft composed of lifeless corneum, from the sides of which extend the parallel barbs. The proximal end of the shaft, which is bare of barbs and hollow, is known as the quill. The opening into the proximal end of the quill is the inferior umbilicus, and a similar one at the distal end is the superior umbilicus. The solid portion of the shaft, or rachis, gives rise to the lateral barbs, each of which also gives off smaller lateral branches known as barbules. The barbules are provided with tiny hooks which interlock with those adjoining, thus providing a fairly rigid yet flexible surface on either side of the shaft. These planing surfaces made up of barbs and barbules are known as vanes.

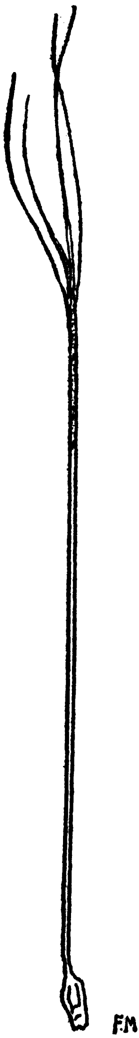


Fig. 147. Pin feather (filoplume).

Feathers may be divided into three main types, namely, quill, down, and pinfeathers. Quill feathers may be further differentiated into tail, wing, and contour feathers. Of these, the tail and wing feathers are heavier and more rigid and play an important part in locomotion through the air. The contour feathers are more generally distributed over the surface of the body. Down feathers (Fig. 146) are small and delicate structures, quite generally distributed between the contour feathers. A typical down feather consists of a short shaft, with a few long and flexible barbs growing from its distal end. The barbs are provided with barbules which are not interlocking. Pinfeathers (Fig. 147), or filoplumes, are stiff, hairlike feathers, with a long shaft having a few terminal barbs.

Although in most forms the surface of the body appears to be entirely covered with feathers, they are really located in definite tracts known as pterylae, with bare areas, the apteria, in between (Fig. 148). All of the feathers taken together constitute the plumage. As is the case with many epidermal structures, feathers are shed periodically, and a new coat replaces them. This process is known as moulting, and should not be confused with ecdysis, during which the entire outer layer (corneum) of the skin is periodically cast off.

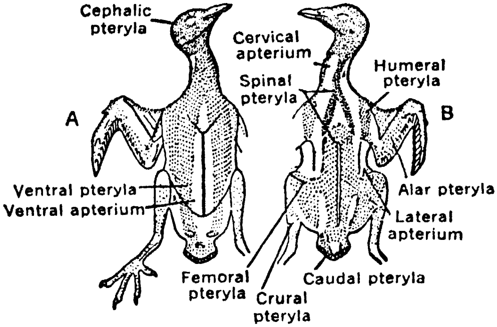


Fig. 148. Feather tracts of the pigeon. A, ventral; B, dorsal. (From Nitzsch; redrawn from Hegner *College Zoology*, by permission of The Macmillan Company, publishers.)

Such heavy structures as scales are not at all common in the skin of birds. When present, they are confined to such regions as the surfaces of the legs (Fig. 149) and the base of the beak. They are of the reptilian type, being derived from the epidermis. The beak itself is an epidermal structure formed in a similar manner. As mentioned above in connection with the similar structures seen in the turtles, the beak partially takes the place of the lost teeth.

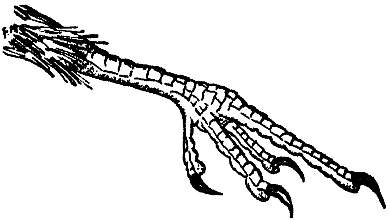


Fig. 149. Foot of pigeon, showing scales and claws.

Integumental glands also are conspicuous by their absence in the members of this class. About the only known structures of this kind are the oil glands in the cavity of the external ear of the turkey and other gallinaceous birds, and the so-called uropygial glands present in most of the flying birds. The latter are paired glands located at the base of the tail. Their main function at the present time seems to be the secretion of an oil used in preening the feathers, although there is some evidence pointing to a former association with sex attraction.

The claws of birds are essentially similar to those of the reptiles, but subject to much variation associated with life in different habitats. Although in most cases the claws are confined to the toes, there are some interesting exceptions to this condition. The fossil remains of the oldest known bird, *Archeopteryx*, show the presence of three claws on the ends of the digits forming the wing, while some of the existing running birds have claws on the first and second digits of the fore limb (Fig. 150).

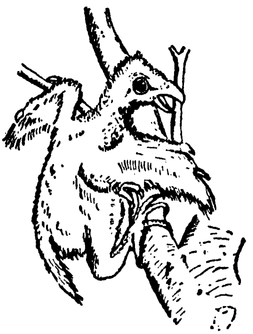


Fig. 150. Young hoactzin, climbing a tree by means of claws on wings. (From Walter, *Biology of the Vertebrates*, after Lucas, by permission of The Macmillan Company, publishers.)

Finally, among the integumentary structures of the class Aves may be mentioned the pointed horny spurs upon the legs or wings of the male in some species. These are used as defensive or offensive weapons.

MAMMALS. The vertebrate integument with its various derivatives reaches its highest development in the mammals. As seen microscopically, the mammalian skin consists of the typical layers which have been described above (Fig. 151). The corium, which in some forms is much thicker than the epidermis, is used in the preparation of leather. The thinnest region of the skin is that which passes over the exposed part of the eyeball. This is known as the conjunctiva. The thickest areas are those of the soles of the feet.

The most noticeable derivative of the mammal skin is hair. Although there are a few exceptional forms having very little hair, its presence is as characteristic and distinctive of the class as feathers are of birds. Noteworthy among the apparently hairless forms are the elephant with a small tuft of hair at the end of the tail, the rhinoceros and the hippopotamus with a few coarse bristles around the snout, and the members of the aquatic orders Sirenia and Cetacea, the embryos of which are covered with a coat of embryonic hair, the lanugo.

The hair develops (Fig. 152) entirely from the epidermis, appearing first as an invagination of the Malpighian layer.

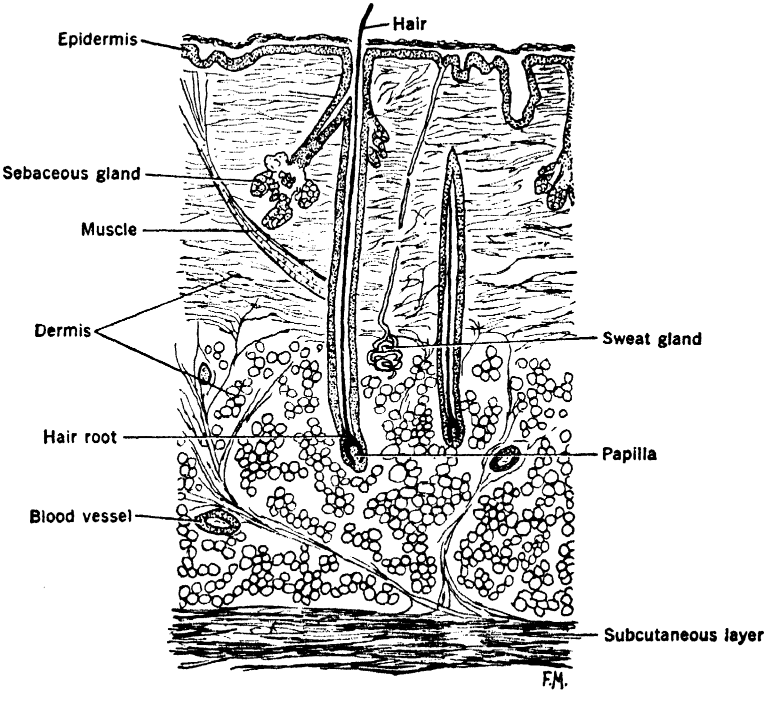


Fig. 151. Diagram of a section of mammalian skin, showing histology.

This dips into the corium as a solid column of rapidly multiplying cells, the outer layers forming a sheath or follicle and the inner cells developing into a horny shaft which projects externally as the hair. A dermal papilla, which projects into the cuplike end of the follicle, furnishes nourishment for the rapidly multiplying cells which keep up the growth of the horny shaft.

The character (Fig. 153) and distribution of the hair is subject to much variation throughout the class. In the hog, for example, it is present in the form of relatively coarse bristles. In the hedgehog (Fig. 154) and porcupine, numerous individual hairs are joined together to form the characteristic spines or quills (Fig. 155). The "horn" of the rhinoceros is formed in this way by the fusion of a group of adjacent hairs.

It may be stated as a general principle that those forms living in tropical or temperate regions are less completely covered with hair than are those living in the arctic zones. The return to the water has evidently brought about almost complete loss of hair, as is illustrated in the members of the fully aquatic orders. In the semiaquatic, or amphibious, seal and otter, it has been reduced to a coat of soft, fine plush. Much racial variation in man is also apparent, ranging from the hairy native of Australia to the beardless Malays. The excessive growth of hair in local regions is of frequent occurrence in various mammals. Among such growths may be mentioned the mane of horses, the beard and long hair of the head and the axillary and pubic regions of man.

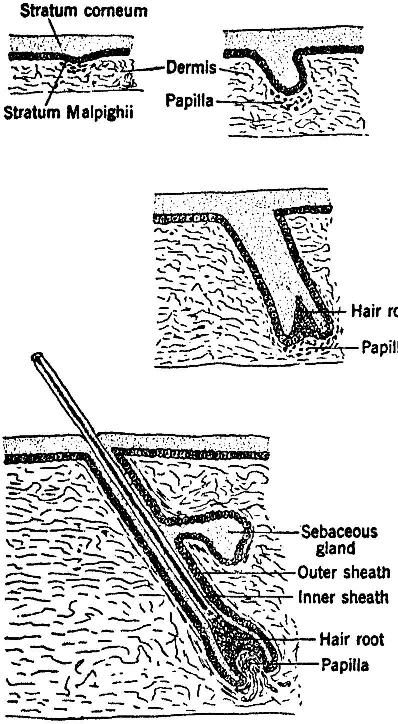


Fig. 152. Diagrams showing the development of hair. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

The mammalian skin is also plentifully supplied with several types of glands which have evidently developed in relation to the hair. Although subject to much later variation, these glands are of two main types, the sweat and the sebaceous glands.

The sweat glands are usually of the simple tubular type and are often coiled (Fig. 151). Physiologically, they are spoken of as vitally secretory since they continue to produce their secretion without using up the substance of the cells of which they are composed. Sweat glands are present in all mammals with the exception of a few forms, among which may be mentioned *Echidna*, the spiny anteater; *Manis*, the scaly anteater; *Chrysochloris*, the Cape Golden mole; *Talpa*, a common mole; and the members of the aquatic orders, Sirenia and Cetacea. The secretion of these glands is typically a colorless, watery fluid containing various waste products of metabolism. They may therefore be considered as having an excretory function. The sweat of the hippopotamus and of the giant kangaroo is reddish in color, while that of *Cephalopus*, a South African antelope, is bluish.

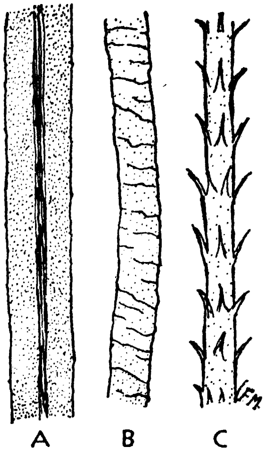


Fig. 153. Three kinds of hair. A, human; B, sheep; C, bat.

The ② sebaceous glands differ from the preceding both morphologically and physiologically. Anatomically, they

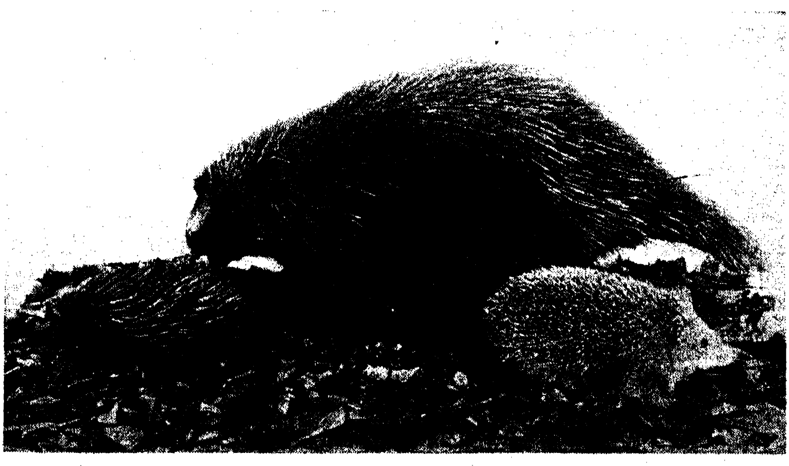


Fig. 154. A group of spiny-skinned mammals. Left, *Echidna*, the spiny anteater; center, *Erethizon*, the Canada porcupine; right, *Erinaceus*, the European hedgehog. (Courtesy American Museum of Natural History.)

are of the compound alveolar type, and with respect to their activity they are known as necrobiotic in contrast to the vitally secretory type. In a necrobiotic gland the individual cells liberate their secretions by breaking up and are thus destroyed. The primary function of the sebaceous glands seems to be that of furnishing an oily secretion for the hair.

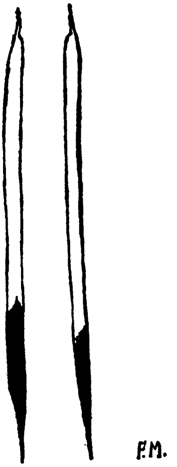


Fig. 155. Porcupine quills.

Sebaceous glands are missing in the Sirenia and Cetacea and in such individuals as *Choloepus*, the two-toed sloth; *Chrysochloris*, the Cape Golden mole; and *Manis*, the scaly anteater. A number of modified glands of this type are found unconnected with a hair follicle. Among these are the Meibomian glands of the human eyelid. These are enlarged sebaceous glands of the eyelashes, which secrete a line of oil at the edge of the eyelid, thus preventing normally the overflow of tears. Other modified glands of this type are found near the various openings of the body, such as the lips, the anus, and external genitals.

A number of mammals possess various kinds of scent glands of this same type as far as structure is concerned. The best known of these are perhaps the anal glands of the skunk, which discharge into the rectum an ill-smelling defensive fluid. Other glands of this nature secrete odoriferous fluids such as musk and civet, for the purpose of sexual attraction.

4 The ceruminous, or wax, glands in the external ear passage are of the tubular type, but resemble the sebaceous glands in producing an oily material that serves to prevent the entrance of foreign objects into the ear.

Equally distinctive of mammals as a class are the mammary or milk-producing glands to which the name of the group refers. These were formerly thought to be modified sweat (monotremes) or sebaceous (other mammals) glands. In structure they resemble sweat glands, and it is probable that both were derived from a common tubular type. In nearly all mammals, their activity is confined to the female and then is periodic rather than continuous. The secretion of these glands is the natural food of the young mammal. In the monotremes the milk glands appear as a pair of depressed oval areas on the abdomen. Each area contains many lobules each of which is composed of branching tubular glands. The lobules open directly upon the surface through pores which accompany hair follicles. It has been generally believed that the secretion is licked from the adjoining tufts of hair with the aid of the protrusible tongue.

In other mammals, the glands are provided with elevated nipples, or teats, that contain the outlets for the ducts. In many forms the nipples are located on swellings of the integument, known as breasts or mammae. In placental mammals the nipples are arranged in two longitudinal rows, and the number is subject to much variation, depending upon the loss from different regions of these longitudinal rows. In man, the horse, elephant, etc., a single pair of nipples remain, while the number may reach as high as twenty-four in certain other forms. Where reduced to a single pair, or to two pair, they are confined to the pectoral or inguinal region; when more numerous, they occur in paired rows along the length of the abdomen.

The presence of supernumerary nipples in man is known as hyperthelism; the presence of extra breasts as hypermastism. These conditions may be considered as evidences of evolution. The functional activity of mammary glands occurs exceptionally even in man. This condition, known as gynecomastism seems to be the normal condition in the monotremes.

In early embryonic development the nipples appear as two longitudinal elevations, known as milk-ridges, on either side of the median ventral line, extending from the pectoral to the pelvic region. Each nipple sinks inward in the form of an epithelial thickening which gives rise to the milk gland. In most mammals, papillae from within these depressions evert to form the nipple. This type has been called an eversion nipple (Fig. 156F). A different type, known as the proliferation nipple, is formed in the ungulates. In these animals a large part of the nipple is formed by an elevation of the surrounding skin (Fig. 156C). These two types were formerly known as true and false nipples, respectively. Since the ungulate nipple is not formed exclusively from the skin, and since its cavity is the outlet of the milk glands, there seems to be no good reason for considering it a false nipple.

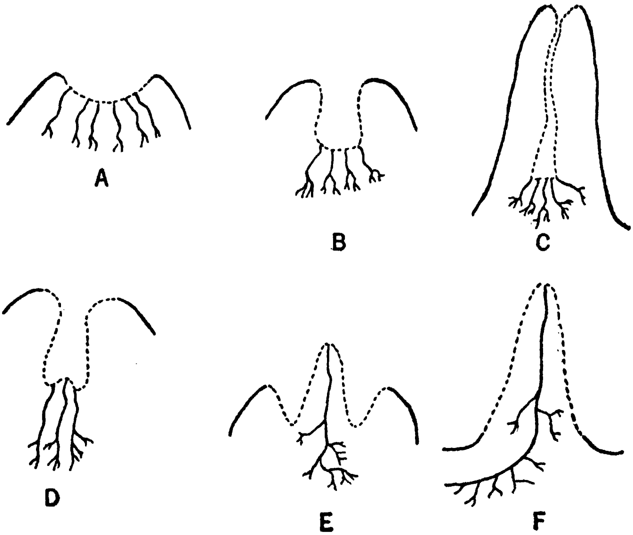


Fig. 156. Types of nipples. A, *Echidna*, primary condition; B, calf (embryo); C, cow (adult) false nipple; D, *Halmaturus*, a marsupial; E, *Didelphis* (opossum) before lactation; F, *Didelphis*, during lactation. The glandular area is indicated by dotted lines. (Redrawn from Wilder, *The History of the Human Body*, after Weber, by permission of Henry Holt and Company.)

The claws of mammals (Fig. 157) consist of the two plates, unguis and subunguis, as previously described. In *Echidna*, the claw is of the reptilian type with dorsal and ventral plates approximately equal. From this condition there is seen a tendency toward a reduction in the size of the subunguis and a flattening of the unguis (Fig. 158). The culmination of this tendency is found in the nail of

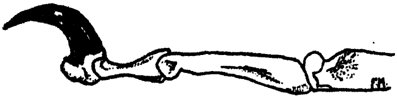


Fig. 157. Digit of carnivore. *Canis sp.*, a coyote, showing claw.

primates (Fig. 159), which consists very largely of a flattened unguis. A different development is seen in the hoofed

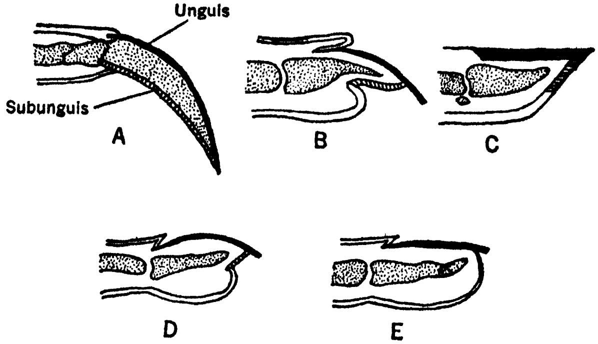


Fig. 158. Longitudinal sections of mammalian digits showing claws, nails, and hoofs. A, *Echidna;* B, a typical carnivore; C, horse; D, monkey; E, man. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company. A, after Gegenbaur; B–E, after Boas.)

mammals (Fig. 160). In these forms the subunguis forms a horny surface, more nearly at right angles to the unguis, for contact with the ground. In many carnivores, the claws are curved and sharp pointed. In the cat, they are retractile, being provided with a protective sheath into which they may be withdrawn. The claws of the bats and sloths are in the form of long and curved hooks, of use when suspending the body upside down from the branches of trees. In the lemurs, the second digit of the foot is furnished with a claw, while the other digits are equipped with rounded nails.

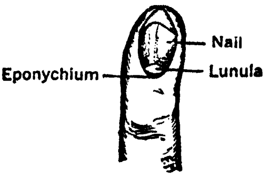


Fig. 159. The human nail.

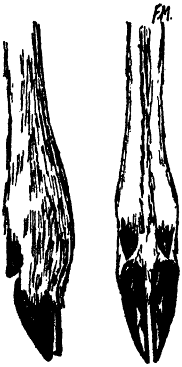


Fig. 160. Foot of a deer, showing hoof.

Associated with the digital tips of mammals are areas of thickened corneum on the ventral surface just behind the subunguis. These cushions, or apical pads, form surfaces upon which the weight of the animal is borne.

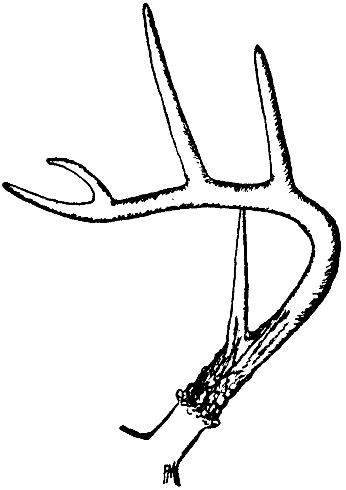


Fig. 161. The antler of a deer.

Horns are, in part, epidermal structures confined, among living vertebrates, almost exclusively to the hoofed mammals. There are four types, known as keratin fiber horns, antlers, pronghorns, and hollow horns. Keratin fiber horns are entirely epidermal, being composed of numerous keratin fibers cemented together. This type of horn is found in the rhinoceros. Antlers (Fig. 161) are characteristic of the deer family and, with the exception of the reindeer, are found in the male only. An antler consists of bone which grows out from the skull. For a time the bone is covered over by an epidermal layer, in which condition it is said to be "in velvet" (Fig. 162A). The skin later dries and becomes worn off, leaving the bone uncovered. It is, therefore, only when the antler is "in velvet" that any portion of it may be considered an epidermal structure. In the giraffe the short single antlers remain throughout life and are permanently "in velvet." In other forms the antler is shed each year and a new one develops bearing an additional prong.

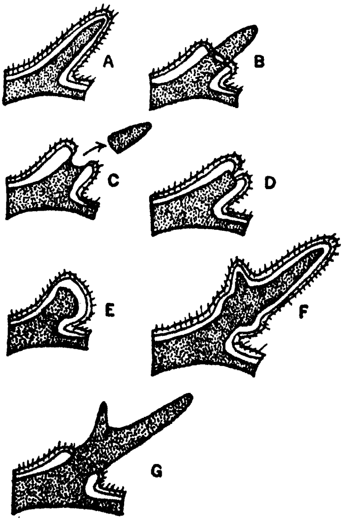


Fig. 162. Diagrams showing the growth and shedding of antlers. (Redrawn from Walter, *Biology of the Vertebrates*, after Nitsche, by permission of The Macmillan Company, publishers.)

The pronghorn (Fig. 163) differs from the antler in that the bony core is a permanent structure, while the outer sheath of horny integument is shed periodically. A horn of this type is found in the American pronghorn antelope, *Antilocapra americana.*

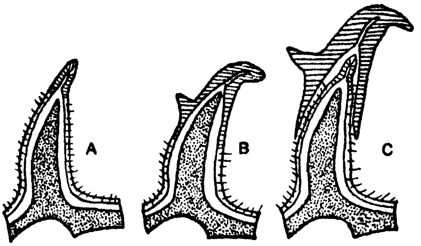


Fig. 163. Diagrams showing the formation of the pronghorn. (Redrawn from Walter, *Biology of the Vertebrates*, after Nitsche, by permission of The Macmillan Company, publishers.)

The hollow type of horn (Fig. 164) is characteristic of cattle, sheep, goats, and antelopes. It is an epidermal structure derived from the Malpighian layer and fits over a bony core which is an outgrowth of the frontal bone of the skull. It is a permanent corneal structure that is renewed from within as the outer surface wears away. The hollow horn is usually present in both sexes.

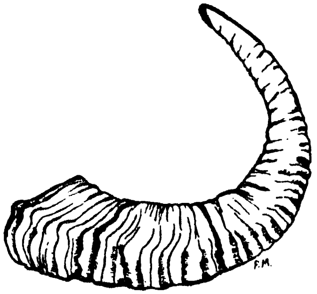


Fig. 164. The hollow horn of the "big-horn sheep."

Another type of structure derived from the integument in mammals is the so-called whalebone (Fig. 165) of the toothless whales. This is not bone at all, but an epidermal structure in the form of horny plates which are suspended from the upper jaw, forming a fringe which serves the purpose of a strainer for the small organisms upon which these animals feed.

FUNCTIONS OF THE INTEGUMENT

At the beginning of the discussion of the vertebrate integument, it was described as a compound organ having a variety

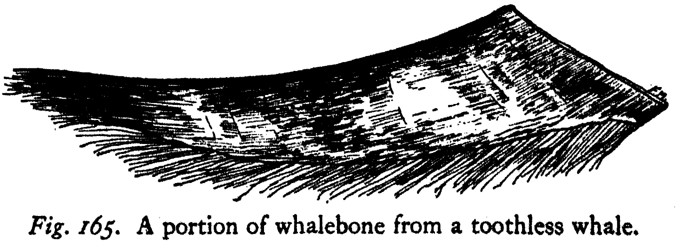


Fig. 165. A portion of whalebone from a toothless whale.

of functions. Some of the important functions should be apparent after reading the pages following that statement.

1. The primary function of the skin is undoubtedly that of protection. Aside from the obvious defense afforded by such derived structures as scales, spines, etc., the skin, if unbroken, forms a practically germproof membrane covering the entire body.

2. The activity of the various glands located in the skin makes it an important secretory structure. It reaches its maximum of importance in this respect in the mammals, because of the activity of sebaceous and mammary glands.

3. We have seen also that in some vertebrates, particularly the amphibia, the skin is an important respiratory membrane.

4. Deposits of fat stored in the deeper regions serve as reserve deposits of food material.

5. Through such derivatives as the teeth, the digestive process is furthered in the mechanical preparation of food material.

6. The feathers of a bird are important organs of locomotion, while folds of skin in the bats, flying squirrels, *Galeopithecus*, and others, in a less satisfactory manner, serve a similar function.

7. In mammals through the activity of the sweat glands, the skin becomes an organ of excretion.

8. It was seen also that some of the specialized glands are accessory reproductive organs, directly in the case of those related to the external genitalia, and indirectly in those associated with the attraction of the sexes.

9. In the development of the dermal bones of the skull, the integument contributes to the formation of the skeleton.

10. And finally, the skin plays the part of an important sense organ because of the presence in it of large numbers of sensory nerve endings as well as of many simple sense organs.

SUMMARY

The vertebrate skin is a double organ having many important functions, and giving rise to a variety of structures. It consists of two regions, epidermis and dermis, each containing several layers of cells. The epidermis is derived from the ectoderm and consists of various kinds of epithelial cells. The dermis is derived from the mesoderm, consists largely of connective tissue, and gives rise to numerous structures.

The skin of cyclostomes contains many single-celled glands which produce a mucus secretion. In Petromyzon a series of "horny teeth" are formed in the epidermis.

The skin of fishes is characterized by the presence of numerous scales of various types — placoid (dermis), ganoid (dermis), cycloid (dermis), and ctenoid (dermis). Glands and pigment cells are also present. Ceratotrichia are horny threads found in the fins. Certain bones are formed within the dermis of fishes and in all forms above them.

The amphibian skin contains numerous many-celled glands and pigment cells. Scales are present in the order Gymnophiona only.

In the reptiles, the skin is marked by the presence of numerous scales (epidermal) and by the absence of glands. Claws (epidermal) are present at the ends of the digits in most members of the class. Such specialized structures as spines, horns, beaks, and rattles are found in the skin of certain reptiles.

The most characteristic structure in the bird skin is the feather. This is of epidermal origin. Claws are present in the feet of many species. Scales are found on the legs of certain forms, and a beak is present.

The mammalian skin contains a variety of structures such as hair, glands (sweat, sebaceous, scent, and mammary), digital tips (claws, nails, and hoofs), horns (fiber, antler, prong, and hollow), and whalebone.

VII. The Skeleton

The skeleton of the vertebrates is an endoskeleton. With the exception of the few exoskeletal structures of epidermal origin described in the preceding chapter, the vertebrate skeleton is an internal structure composed of living tissue. It is derived as a modification of mesenchyme, the notochord excepted, and is, therefore, of mesodermal origin. Practically all skeletal structures are formed from groups of mesenchyme cells, the sclerotomes (Fig. 7), which have budded off from the inner walls of the mesodermal segments. This mesenchyme invades all available space between other structures and from it the skeletal tissues are derived.

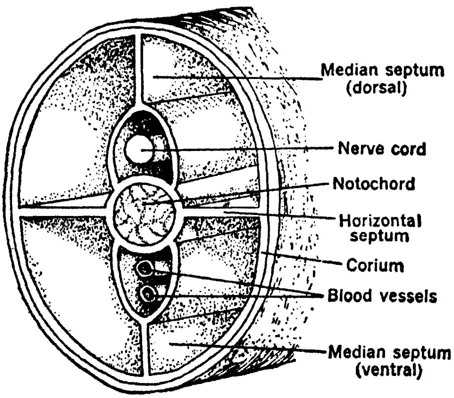


Fig. 166. Diagram of a cross section through the tail region of a vertebrate, showing the skeleton-forming tissues and their relations to other organs. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

ORIGIN

This continuous mass of mesenchyme has been referred to as the membranous skeleton, and within its limits are formed the supporting tissues of the body (connective tissue) and the true skeletal tissues, cartilage and bone. Among the more important regions (Fig. 166) giving rise to parts of the skeleton are the corium, or the inner layer of the skin; the vertical median septum; the horizontal septum; and the myosepta. The corium has been discussed in the chapter on the integument, where the development of true bone was mentioned in the case of the dermal bones of the skull. The vertical median septum is a thin plate of connective tissue extending between dorsal and ventral surfaces, passing on either side of the nerve cord and notochord. Dorsal to the nerve cord and also ventral to it in the tail region, this septum lies in the sagittal plane. In the region of the body cavity it is interrupted ventrally and divides to pass anteriorly on either side of the cavity just outside the peritoneum. The horizontal septum is a similar sheet extending from the corium to the median septum and dividing the myotomes of either side into dorsal (epaxial) and ventral (hypaxial) groups. The myotomes are separated from one another by vertical (transverse) partitions, the myosepta, which are continuous with the other mesenchymatous septa just described. In these regions and particularly at the junction of the various sheets of tissue, the parts of the vertebrate skeleton are formed.

SKELETAL TISSUES

The important skeletal and supporting tissues of the body are connective tissues (Fig. 167), cartilage (Fig. 168), and bone (Fig. 169). To these three may well be added the notochord, if we bear in mind that it is present as an important part of the adult skeleton in the cyclostomes only. In all other vertebrates it is merely a temporary skeletal axis which is later replaced by bony or cartilaginous units. The formation of these units takes place in the sheaths immediately surrounding the notochord rather than in the notochord itself.

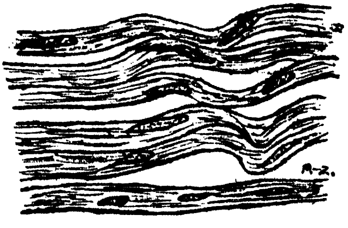


Fig. 167. Connective tissue from cornea of the eye.

Connective tissue. Although this kind of tissue is a supporting rather than a true skeletal tissue, it is conveniently described here as so many skeletal structures are developed within its limits. In its development from mesenchyme, the cells become flattened or spindle-shaped. Associated with these cells, within the matrix (the substance filling the intercellular spaces) various types of fibers develop which eventually largely obscure the individual cells. In loose connective tissue, such as may be found between the muscles, the fibers form a spongy network of delicate filaments. In dense connective tissue of the type forming the dermis of the skin, the fibrils are often bound together in bundles forming a tough network. Other fibers, known as elastic fibers, also are common in connective tissue. An elastic fiber is a structureless thread which is not composed of smaller fibrils.

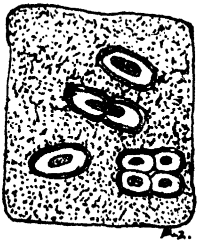


Fig. 168. Cartilage.

Ligaments, the tough bands of tissue between bones, are composed largely of elastic fibers. The term fascia is applied to the thin sheets of connective tissue surrounding muscles. A tendon may be defined as a thick, narrow band of connective tissue by means of which various muscles are attached to parts of the skeleton.

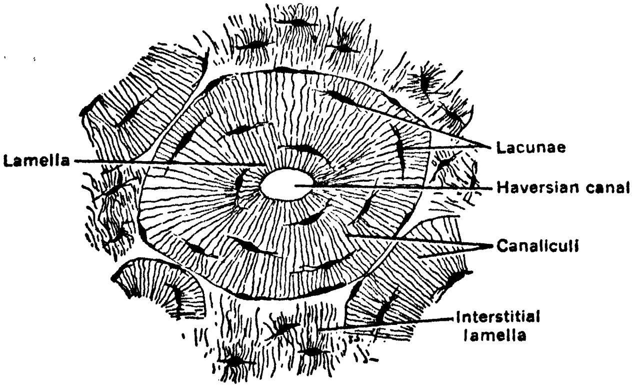


Fig. 169. Cross section of bone.

CARTILAGE. This tissue is also a derivative of mesenchyme. In its development it passes through a stage in which it is known as precartilage. In this stage the large cells are closely adjacent to one another, instead of being separated by the intercellular spaces characteristic of mesenchyme. The precartilage is surrounded by a layer of connective tissue, the perichondrium. In cartilage, the fluid substance between the cells of the precartilage stage has been changed to the form of matrix characteristic of this tissue. The formation of the matrix is not well understood, but it is probably the result of some kind of cell secretion. The cartilage cells lie in spaces, the lacunae, within the matrix. The matrix is formed around perichondrial cells nearest the cartilage already formed, and in this way the extent of the tissue is increased.

There are three principal forms of cartilage, known as hyaline, elastic, and fibrous cartilage. Hyaline cartilage is perhaps the commonest type. Its cells are embedded in a clear translucent matrix, usually free from fibrils. In elastic cartilage, fibers or networks of elastic substances are present in the matrix, giving it a characteristic yellow color. This form develops from hyaline cartilage. Fibrocartilage consists very largely of interwoven bundles of white fiber. It resembles dense connective tissue, except that the cells are arranged in lacunae within the matrix as in the other forms of cartilage.

BONE. Two kinds of bone may be distinguished — cartilage or replacing bone, and dermal or investing bone. The difference between these two types is one of origin rather than of structure. Cartilage bone is formed in cartilage, which it eventually replaces, while dermal bone develops in the deeper layers of the skin. The latter type has been referred to previously in the chapter on the integument in connection with the development of the ganoid scales. In the formation of cartilage bone, certain cells known as osteoblasts secrete lime salts and a substance known as ossein. These materials replace the organic substance (chondrin) of which the cartilage was composed. In the development of dermal bone certain of the connective tissue cells function as osteoblasts and secrete ossein and lime directly. The cells surrounding these bone-forming elements make up the periosteum.

Bone tissue, whatever its origin, consists of living bone cells, which lie in lacunae, surrounded by the matrix (Fig. 169). The cells are grouped in concentric rings, the lamellae, surrounding a central cavity, the Haversian canal. The lacunae are in communication with one another as well as with the Haversian canal, by means of microscopic tubes, the canaliculi, which penetrate the matrix. The Haversian canals form passageways for blood vessels, lymphatics, and nerves, which supply the living bone cells.

THE PARTS OF THE SKELETON

The vertebrate skeleton may be divided, for convenience of description, into two main divisions, the axial skeleton and the appendicular skeleton. The axial skeleton includes the skull, the visceral arches, the vertebrae, the ribs, and the sternum. The visceral arches, which develop in relation to the pharyngeal pouches, are sometimes referred to as the splanchnocranium. This contrasts with the neurocranium, which develops in relation to the brain. Parts of the splanchnocranium (the upper and lower jaws) become closely attached to the neurocranium in the adult skull of the higher vertebrates. The appendicular skeleton consists of the bones or cartilages of the paired appendages and of the girdles which support them.

The Axial Skeleton

VERTEBRAE. As previously mentioned, the vertebrae are cartilaginous or bony units, elements of which appear for the first time in vertebrate history among the cyclostomes. In this class they consist merely of small cartilages, originating just lateral to the notochordal sheath and projecting dorsally to afford some slight protection to the sides of the nerve cord. In the cartilaginous fishes, these units are much more complete, having united dorsal to the nerve cord, to form a complete neural arch (Fig. 176). A similar haemal arch is found ventral to the notochord in the tail region. Growth has also taken place in all directions around the notochord, resulting in the formation of a series of rings around this axial rod. In all other vertebrates, with the exception of certain fishes found among the other orders, the vertebrae are composed entirely of bone, while the notochord has been almost completely replaced.

A typical vertebra. A human lumbar vertebra (Fig. 170) may be described since it contains the parts characteristic of a typical vertebra. The main part of this bone consists of a thick, rounded disc known as the centrum. Directly above the centrum is an opening, the neural canal, through which, in the living animal, the nerve cord passes. The canal is enclosed by a thin wall of bone, the neural arch. This is extended dorsally into a median, pointed projection, known as the spinous process (neural spine). A pair of similar projections, extending laterally from the sides of the arch, are the transverse processes. At the base of the spinous process are pairs of similar but smaller structures projecting anteriorly and posteriorly. These are known as zygapophyses (articular processes), the anterior pair being the prezygapophyses, and the posterior the postzygapophyses. On these zygapophyses are smooth surfaces or facets by means of which the successive vertebrae articulate with one another. These are, respectively, the cranial and caudal articular facets, the former facing forward, upward, and inward, the latter backward, downward, and outward.

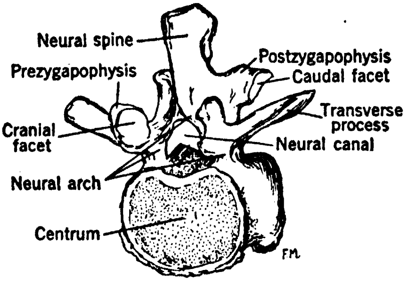


Fig. 170. Human lumbar vertebra, showing the parts of a typical vertebra.

There is much variation from this type in details of structure, not only in the various members of the different groups of vertebrates but in the different regions of the vertebral column in the same species. This differentiation of vertebrae will be considered more fully on subsequent pages.

Development of the vertebrae. It is very difficult to describe the complex development of a vertebra within the limits of a short text in vertebrate anatomy. Although much research has been done in this field, there is still much difference of opinion concerning the details of the embryonic development of a vertebra. This is especially true in the case of the centra, as their components apparently vary greatly in the different vertebrates. In the following brief account of this development, only the more generally accepted facts will be presented.

As mentioned in Chapter V, the origin of a vertebra may be traced back to the segmentally arranged mesenchymatous sclerotomes (Fig. 171). These metameric bodies are quite definitely subdivided into a cranial and a caudal portion. The posterior or caudal half becomes much denser in appearance. Between the sclerotomes are located the intersegmental blood vessels. The mesenchyme of the sclerotomes migrates in various directions, such as around the notochord and nerve cord and along the various septa.

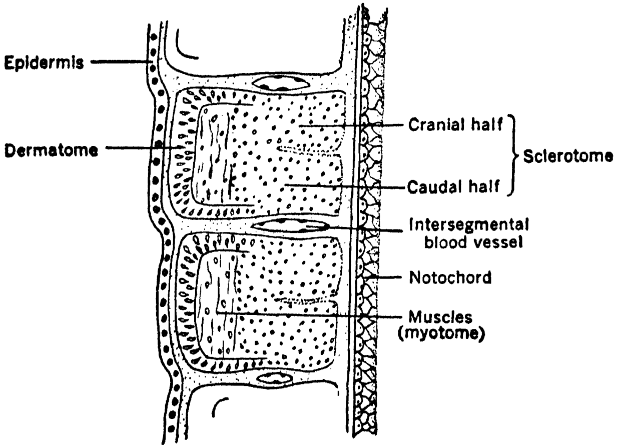


Fig. 171. Diagram showing developing sclerotome halves in a lizard, *Sceloporus*. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

The beginnings of the vertebrae are seen in the small paired cartilages which develop within the cranial and caudal halves of the sclerotomes (Fig. 172). These cartilages, which are known as arcualia, are eight in number in each sclerotome. Two of these on each side are located dorsally, the other two ventrally. The anterior dorsal pair are known as interdorsals; the anterior ventral pair as interventrals; while the posterior and larger dorsal pair are the basidorsals, and the posterior and larger ventral pair are the basiventrals. In the subsequent development of these cartilages, the basidorsals extend dorsally around the nerve cord and unite above it to form the neural arch. In a similar manner, the basiventrals in the tail region surround the blood vessels to form the haemal arch.

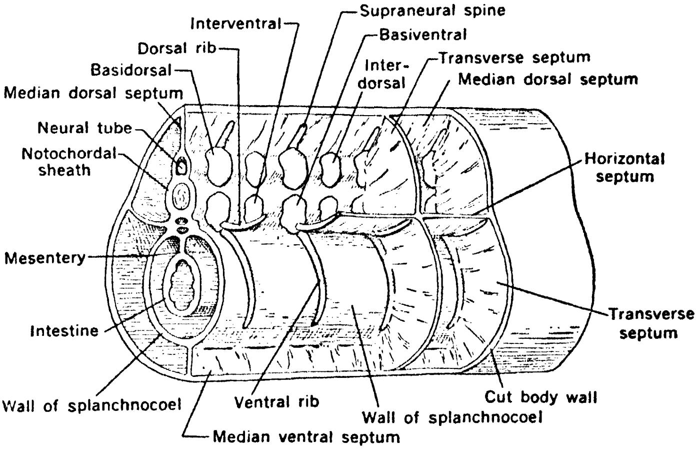


Fig. 172. Diagram of the connective tissue system in the trunk of a vertebrate, showing the relation between the parts of a developing vertebra, and the various septa. Oblique view of left side from which the septa have been partially removed. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

The centrum is formed from a number of components. Any of the arcualia mentioned above may extend around the notochordal sheath and contribute to its formation. Among many of the cartilaginous fishes, the basidorsals and basiventrals penetrate the sheath of the notochord, spread out in the sheath, and form a ring-shaped centrum. A centrum thus formed within the notochordal sheaths has been called a chordal centrum. The centrum may also be formed largely from components of the mesenchyme which has gathered around the notochord, outside of its sheaths. Such centra have been called perichordal centra in contrast to the chordal type, although it now seems improbable that such an absolute distinction can be made. In most vertebrates the centrum is formed by a combination of the various kinds of components mentioned above.

Each vertebra is formed from parts contributed by the posterior pair of sclerotome halves plus parts contributed by the anterior pair of the succeeding sclerotome halves. In other words, the posterior halves of a sclerotome become the anterior part of a given vertebra, while the anterior halves of a sclerotome pair contribute to its posterior portions. It will thus be seen that the sclerotomes of two segments contribute to the formation of a single vertebra. The vertebrae develop intersegmentally, that is, on either side of a myoseptum. They thus alternate with the myotomes.

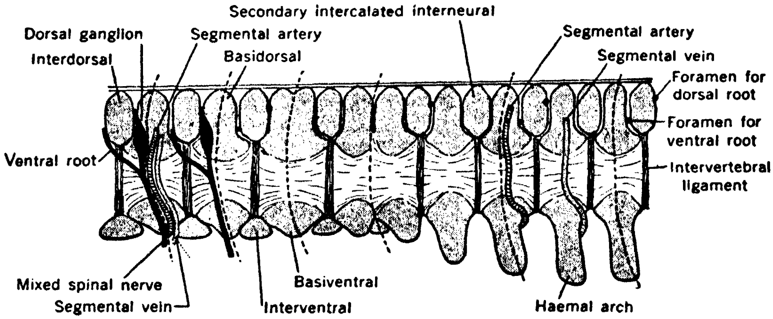


Fig. 173. Diagram illustrating structure of vertebral column and transition to diplospondylous condition in caudal region of an elasmobranch. Cartilage stippled. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

In some cases the components of a vertebra fuse in such a way that two centra are produced in a single segment. This condition, which is known as diplospondyly, occurs in the tail region of *Amia* and various other fishes (Fig. 173).

In the cyclostomes, the neural elements remain in the primitive condition as separate elements on either side of the nerve cord. A complete arch does not appear in the members of this order. The haemal units are present in the tail only and resemble the neurals in that a complete arch is not formed. In general it may be stated that in the forms above the cyclostomes, the dorsal and posterior elements of opposite sides unite above the nerve cord to form a complete neural arch. In the tail region, the haemal arch is formed by a similar union of the ventral and posterior elements, ventral to the caudal blood vessels. The body, or centrum, may be formed by the extension of the bases of some or all of these elements at the sides of the notochord. This extension may spread in all directions, anteriorly and posteriorly, as well as around the notochord. In many fishes, only the caudal elements of each metamere form rings with complete arches. These rings are the centra. The cranial elements are often without arches, and are called intercentra, or intercalaries.

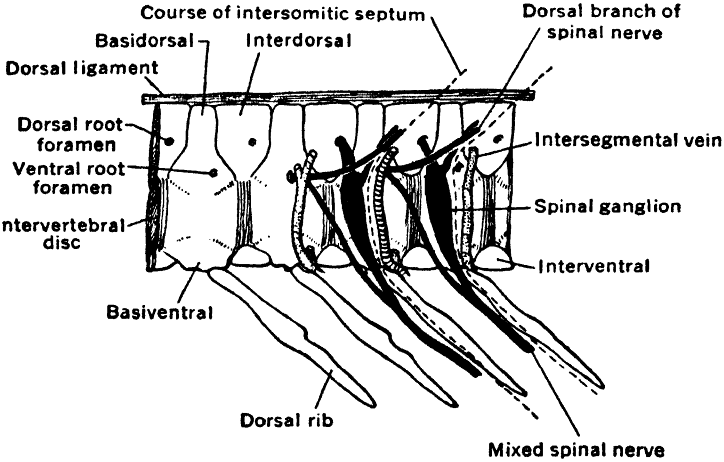


Fig. 174. Squalus acanthias. Left side view of portion of vertebral column of mid-trunk region. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

In the elasmobranchs (Fig. 174) the vertebrae are cartilaginous throughout life. In the Chondrostei and Dipnoi they consist largely of cartilage with some bone formed on the outside. In all other fishes, as well as in the higher vertebrates, the vertebrae are bony units.

The anterior and posterior surfaces of the centra vary greatly in the different groups (Fig. 175). In some, as in the elasmobranchs, both faces are concave. This type is said to be amphicoelous. In some fishes, some amphibia, and many reptiles, the anterior surface is concave and the posterior surface convex. Such vertebrae are known as procoelous, a type having the many advantages of a ball and socket joint.

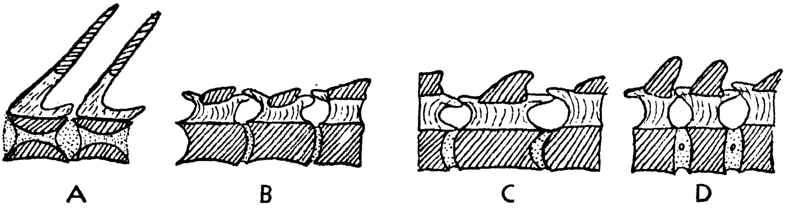


Fig. 175. Diagrams of sagittal sections of types of vertebrae. In Fig. A, the anterior end is at the left; in all others at the right. A, amphicoelous; B, opisthocoelous; C, procoelous; D, acoelous. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

In opisthocoelous vertebrae, the conditions are reversed, the posterior surface being concave. Such vertebrae are not characteristic of any vertebrate class, but occur in many forms in some regions of the column. In the ungulates, for example, the cervical and some of the thoracic vertebrae are of this type. In general, however, the mammalian vertebrae are acoelous, that is, having both surfaces of the centrum relatively flat. The centra do not articulate directly in the mammals, there being discs of fibrocartilage between them.

Differentiation of vertebrae. In most vertebrates the vertebrae vary greatly in the different regions of the body. In the fishes there is little differentiation, except that those in the tail region have a haemal arch (Fig. 176), while all others do not. We may speak, then, of trunk and caudal vertebrae in this class. In the amphibia also, there is little differentiation. In addition to the trunk and caudal vertebrae, there is present for the first time one sacral vertebra. This represents one of the posterior trunk vertebrae which has been modified for the articulation of the pelvic girdle. The most anterior unit of the column forming the articulation with the skull is the atlas. This is the first, and, in this class, the only cervical vertebra. In the order Salientia, the caudal vertebrae have united to form a single bone, the urostyle.

In the reptiles, cervical, trunk, sacral, and caudal regions are well marked, except in the snakes and the legless lizards. The first two cervical vertebrae (atlas and axis) differ markedly from the others in this region. A part of the centrum of the atlas has joined with that of the axis, forming the so-called odontoid process of the latter bone. This forms a pivot upon which the head and atlas turn. In some extinct reptiles, in *Sphenodon*, the crocodile, and certain other living reptiles, an additional bone known as the proatlas is present. This is apparently the remains of a vertebra which was formerly located anterior to the atlas. There are two sacral vertebrae in most living reptiles. In most cases ribs are present on all presacral vertebrae with the exception of the atlas and the axis. The cervicals may usually be distinguished from the trunk vertebrae by the fact that the ribs of the former do not meet the sternum. In the lizards and crocodiles, a further differentiation of the trunk vertebrae into the anterior or thoracic, and the posterior or

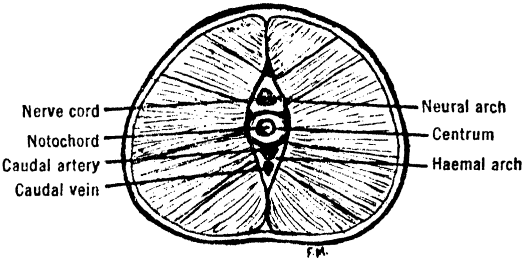


Fig. 176. A cross section of the tail of a dogfish, showing the caudal vertebra.

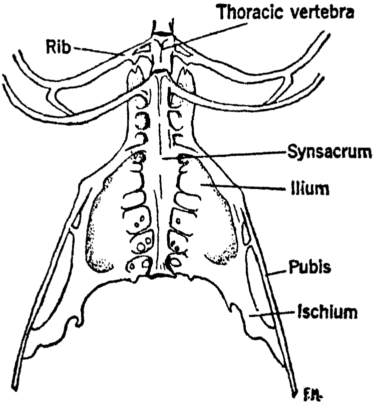


Fig. 177. Synsacrum and pelvic girdle of pigeon, from beneath.

lumbar, is noted. The thoracic vertebrae bear ribs; the lumbar do not.

In the birds, the same regions are always present. The cervicals, including atlas and axis, bear short ribs. The thoracics, six to ten in number, are usually united. In all living birds, the lumbars are united with the two true sacrals, forming the synsacrum (Fig. 177). The caudal vertebrae vary in number from nine to twelve. The more posterior (four to six) of these in the adult unite to form a single bone, the pygostyle (Fig. 178).

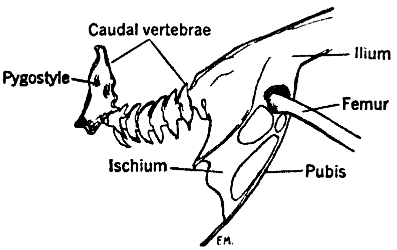


Fig. 178. The pelvic girdle and caudal vertebrae of a bird.

The vertebrae of mammals are usually about thirty-five in number, although the extreme range of variation is from twenty-six to eighty. All five regions are present, except that

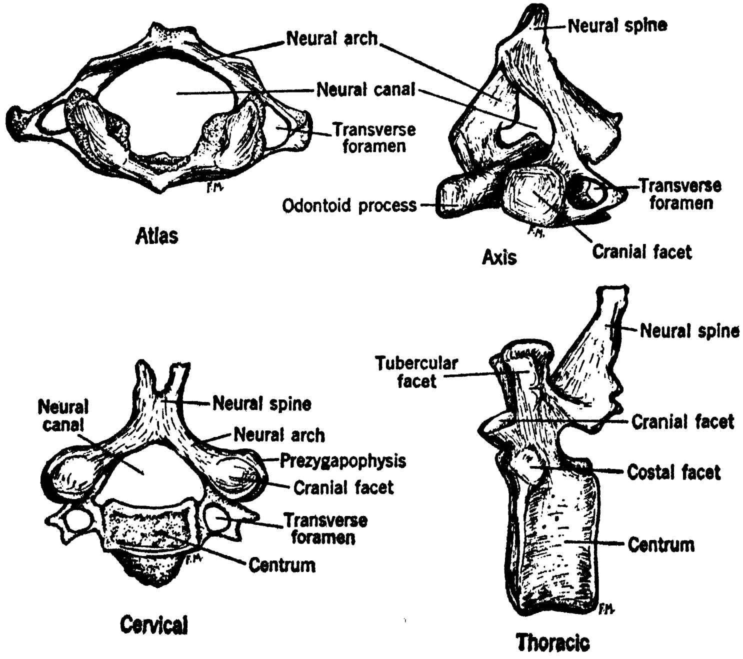


Fig. 179. Human vertebrae.

in the Sirenia and Cetacea a sacrum is lacking. The cervicals are the most constant in number, there being seven in all but four members of the class (*Manatus*, the sea cow, six; *Choloepus*, the two-toed sloth, six; *Bradypus*, the three-toed sloth, nine; and *Tamandua*, the ant bear, eight).

The atlas consists largely of a neural arch and lacks a neural spine. The axis has a large neural spine (Fig. 179) for the attachment of ligaments supporting the cranium. The odontoid process is prominent and may be cylindrical, cone-shaped, or concave dorsally. Its anterior portion, according to embryological studies, represents what is left of the proatlas. The thoracic vertebrae are often thirteen in number (cat), and are characterized by the presence of facets (Fig. 180), for the articulation of ribs. These facets are of two kinds: the costal located on the sides of the centra, and the tubercular, beneath the transverse processes. They articulate, respectively, with the head and the tubercle of the rib. In many forms the costal facet is divided between two vertebrae, the head of a rib articulating with two adjoining vertebrae.

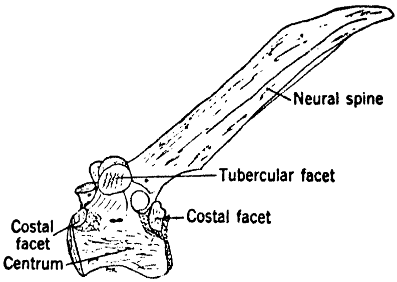


Fig. 180. Thoracic vertebra of cow.

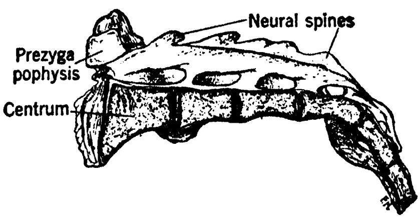


Fig. 181. Longitudinal section of the human sacrum, showing its formation from several vertebrae. (The usual number is five.)

The lumbar vertebrae (Fig. 170) vary from two to nine in number. They are usually large, with heavy centra, prominent neural spines, and transverse processes. There are from two to ten vertebrae usually more or less completely fused, forming the sacrum (Fig. 181). The pelvic girdle articulates with the anterior part of the sacrum (Fig. 182). The caudals vary greatly in number as well as in structure.

The anterior ones differ little from the sacrals, while those nearer the tip of the tail consist of a centrum only. In man but four or five caudals remain. These are more or less fused together, forming the coccyx.

THE RIBS. Two types of ribs (Fig. 183), having an entirely different origin, are found in vertebrates. Both of these develop at the intersection of the various connective tissue septa described above. It should be recalled that the tail and trunk muscles are divided by a horizontal septum into two series, the dorsal or epaxial, and the ventral or hypaxial groups. Ventral to the centra, the hypaxial musculature is divided into right and left muscle masses by a median septum (vertical). In the trunk region, this median septum divides into two lateral septa which pass around the body cavity just outside the peritoneum. These longitudinal septa are intersected at regular intervals by the transverse myosepta, which separate the myomeres. Ventral or pleural ribs are formed at the intersections of the myosepta and the septa just lateral to the body cavity. The second type, the dorsal or intermuscular ribs, develop at the junctions of the myosepta and the horizontal septa, that is, between epaxial and hypaxial muscle masses.

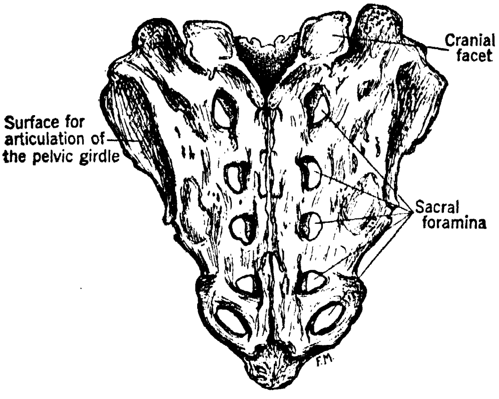


Fig. 182. The human sacrum.

It has long been supposed, and so taught, that ventral ribs were characteristic of fishes while dorsal ribs were typical of most other vertebrates. This is no longer held to be the case as recent studies have shown that ribs, during their development, may change their position in relation to muscles. Consequently the position of a rib in the adult is not necessarily a true indication of its type.

Polypterus has long been noted as having both types of ribs. This same condition is found in the salmon and other teleost fishes. In some fishes additional ribs may be present dorsal to both types.

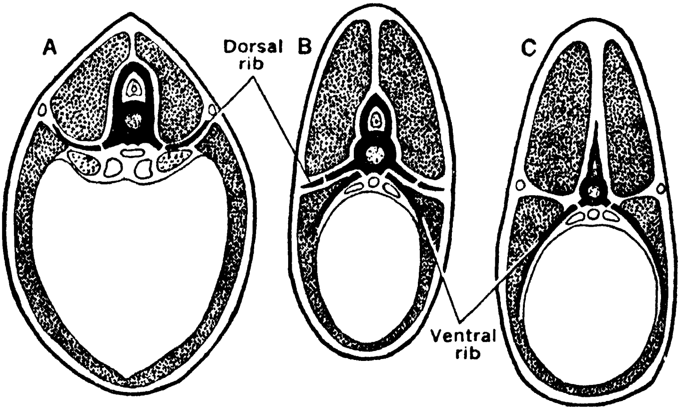


Fig. 183. Diagrams of the two types of ribs. A, elasmobranch with dorsal ribs; B, teleost with both dorsal and ventral ribs; C, amniote with ventral ribs. (From Walter, *Biology of the Vertebrates*, after Coppert, by permission of The Macmillan Company, publishers.)

In the tetrapods, or land vertebrates, there is one pair of ribs to a vertebra. These are now considered to be of the ventral or pleural type. The tetrapod rib is usually a bicipital or two-headed rib. The ventral head or capitulum articulates with a facet on the centrum. The dorsal head or tuberculum articulates with a surface on the transverse process.

In the amphibians the ribs are short and do not reach the sternum. Ribs are numerous in reptiles and birds as they are not confined to the thoracic region. Usually those in the thoracic region are longer, reaching around to the ventral side. In the Crocodilia and some other large-bodied reptiles a series of riblike bones are found ventrally in the lumbar region. These are known as gastralia (Fig. 187) and are of dermal origin (exoskeletal).

In certain lizards similar ventral ribs present in the abdominal region are cartilage bones. These are called parasternals. They are of interest because of their possible relation to the sternum as discussed below.

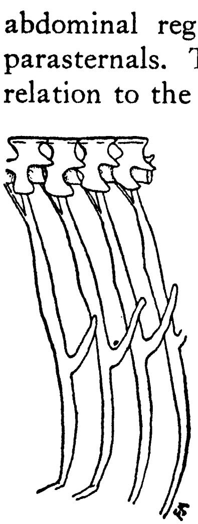


Fig. 184. Ribs of the pigeon showing uncinate processes.

The bird rib is characterized by the presence of the uncinate process (Fig. 184), a rounded projection from the posterior edge of the rib, which overlaps the one following.

In the mammals, ribs are present in the cervical and thoracic regions. In the neck they have united with the centra, while those in the thorax are movable, articulating with the thoracic vertebrae. A true rib is one which reaches the sternum by means of its own cartilage. Most true ribs consist of a dorsal bony part and a ventral cartilaginous portion. The dorsal end of a typical rib (Fig. 185) is known as the head or capitulum. This is separated from a projecting process, the tuberculum (tubercle), by a constricted portion, the neck. The rest of the rib is known as the shaft. The region of greatest curvature of the shaft is known as the angle. False ribs are of two kinds, those which are not directly attached to the sternum, and those which are unattached. The latter kind are also known as floating ribs.

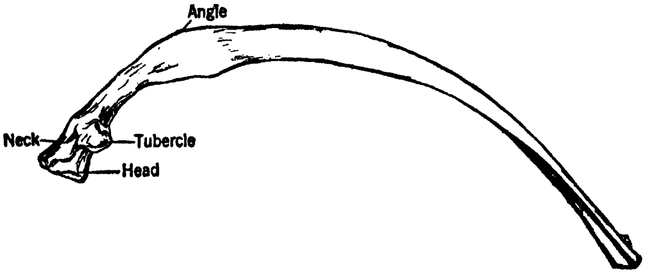


Fig. 185. A human rib.

The number of ribs varies as does the number of thoracic vertebrae. In the cat there are thirteen pairs of ribs of which nine are true and four false. The last pair are floating ribs. In man there are twelve pairs; seven of which are true and five false (two floating).

THE STERNUM. The sternum, or breastbone, consists of a single bone or a series of bones, in the median ventral region of the thorax. Among living vertebrates it is found only in land-living forms. As seen above, the ribs may or may not reach around to the sternum ventrally. It serves to protect the organs of the thoracic cavity, provides attachment for the muscles of the pectoral limb, and aids in respiratory movements. Together with the ribs and vertebrae it forms a part of the axial skeleton often referred to as the thoracic basket.

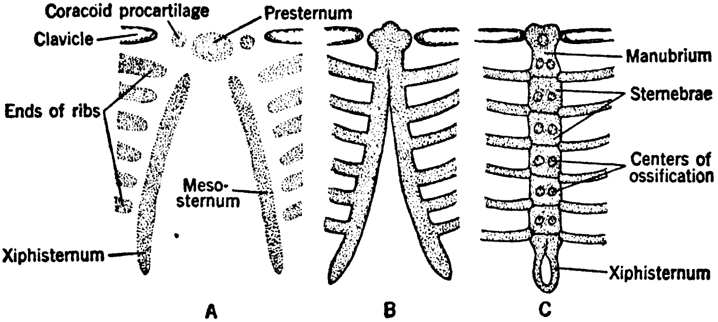


Fig. 186. Diagrams showing development of mammalian sternum. A, early stage; B, cartilage stage, beginning of union; C, later stage, beginning of ossification. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

Phylogeny of the sternum. The evolutionary history of the sternum is still a matter of some controversy. Some have considered it to be derived from the ventral ends of the ribs; others trace its derivation to the pectoral girdle; and it has even been considered to be of independent origin. A more recent theory relates the sternum to those cartilages which develop in the ventral myosepta of certain amphibians and lizards, and which were referred to above as parasternals.

Embryologically, the first appearance of the mammalian sternum is seen in the condensation of a small mass of mesenchyme, in the mid-ventral region between the halves of the pectoral girdle (Fig. 186). This later chondrifies, forming the presternum (prosternum). In a similar manner two elongated bars of cartilage are formed posterior to the presternum extending backward between the free ends of the ribs. These bars later unite with the presternum in front, with one another medially, and with the ribs laterally. The portion uniting with the ribs is called the mesosternum; the free posterior end, the xiphisternum.

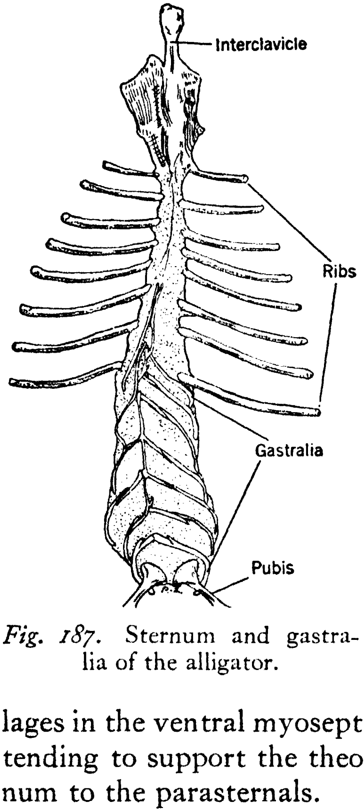


Fig. 187. Sternum and gastralia of the alligator.

Comparative anatomy. In several of the sharks, the Dipnoi, the Caudata, and the lower Salientia, a median cartilage, apparently homologous to the presternum, lies between the coracoid portions of the pectoral girdle. This has been cited as evidence by those who believe in the pectoral girdle theory of the origin of the sternum.

In some of the urodeles, such as *Cryptobranchus*, the sternum is a small cartilage between the posterior portions of the coracoids. In others, for example *Necturus*, it is present in the form of several transverse cartilages in the ventral myosepta. This is considered as evidence tending to support the theory tracing the origin of the sternum to the parasternals.

In the anurans the sternum consists of an anterior portion, the episternum, just anterior to the girdle; and a posterior portion, the xiphisternum, just posterior to it. Each of these consists of a bony and a cartilaginous section.

In *Sphenodon* the sternum is a broad rounded cartilage to which several ribs are attached. In the alligator it is a cartilaginous plate between the ventral ends of the coracoids. This plate is drawn out posteriorly into a pair of xiphisternal horns. The turtles and snakes are without sternal elements.

The sternum of birds is a large, completely ossified, quadrangular or rhomboid bone. In the flying birds the ventral surface is drawn out, forming a median keel, or carina (Fig. 188). This gives additional surface for the attachment of the heavy breast muscles used in flying. In the ratite birds the sternum is rounded or convex ventrally.

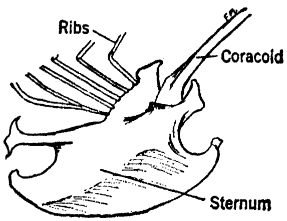


Fig. 188. Sternum of the pigeon.

The sternum of the mammal also is usually ossified. Centers of ossification appear irregularly in the cartilage described above. In many mammals, the anterior portion of the mesosternum unites with the presternum to form a single bone, the manubrium. The remainder of the mesosternum may give rise to a series of separate bones, the sternebrae, or to a single bone (primates), the gladiolus (Fig. 189). The xiphisternum often fails to ossify completely, forming the xiphoid process.

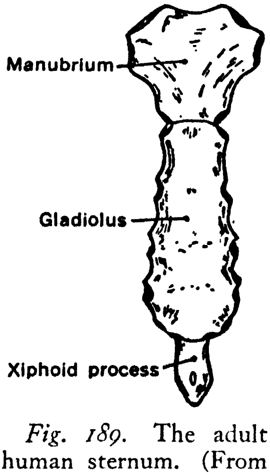


Fig. 189. The adult human sternum. (From Walter, *Biology of the Vertebrates*, after Spalteholz, by permission of The Macmillan Company, publishers.)

THE SKULL (NEUROCRANIUM). The skull is that part of the vertebrate skeleton which surrounds and protects the brain. It has been called the neurocranium in contrast to the splanchnocranium (visceral skeleton), that part which surrounds and protects the anterior part of the alimentary canal. As indicated previously, these two regions of the vertebrate skeleton will be discussed separately, although they are very closely related in the adult of the higher forms.

So much is known concerning the skull from the standpoint of comparative anatomy, embryology, and paleontology, that it is difficult to treat the subject adequately within the limits of a text of this character. The development of the skull of a higher vertebrate so completely portrays its phylogeny that a description of this development makes the most satisfactory introduction to its comparative anatomy.

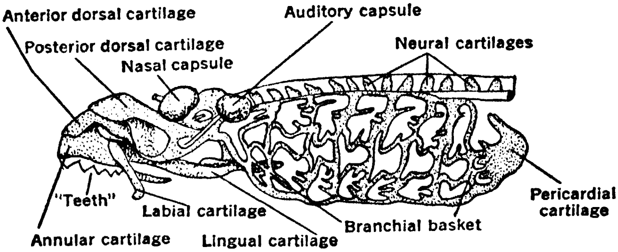


Fig. 190. Lateral view of skull of *Petromyzon.* (Redrawn from Walter, *Biology of the Vertebrates*, after Parker, by permission of The Macmillan Company, publishers.)

Development of the skull. It should be noted first that it is very difficult to compare the skull of the cyclostomes (Fig. 190) with that of all other vertebrates. In this class, the skull consists of a series of cartilages surrounding the mouth and providing slight support for the brain. These separate cartilages have not been satisfactorily homologized with the parts of the skull of other vertebrates. With this

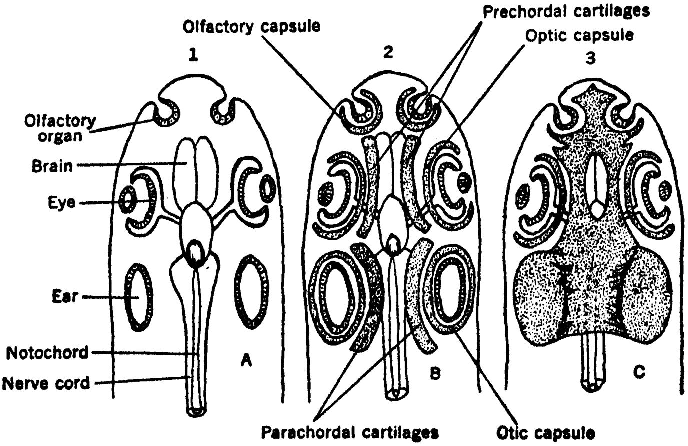


Fig. 191. Diagrams showing the development of the vertebrate skull as seen ventrally. A, notochordal stage; B, underpinning stage; C, fusion stage. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

exception, the skull of a higher vertebrate, during its development, passes through stages in which it typifies successively the adult skull of representatives of the various lower groups.

In most vertebrates, the skull first appears as a series of paired cartilages (Fig. 191). Of these, one pair, the parachordals, are formed at the sides of the notochord. A second pair, the trabeculae, or prechordals, develop in front of the notochord. These four elements increase in size and eventually fuse with one another so that a broad, thin plate is formed surrounding the anterior end of the notochord and supporting the brain from below. A large opening, the hypophysial fenestra, is usually left in front of the notochord. The thin plate of cartilage formed by the fusion of the trabeculae just in front of this fenestra is the ethmoid plate. The posterior portion surrounding the notochord is the basal plate.

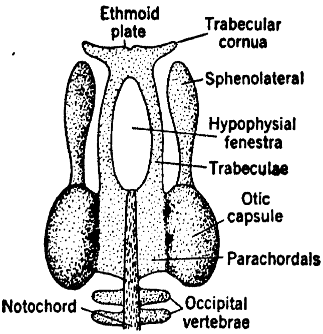


Fig. 192. Early chondrocranium of an elasmobranch. (Redrawn from Kingsley, *The Vertebrate Skeleton*, Blakiston Co., by permission of Miss Mary W. Kingsley.)

While the development described above is taking place, the sense organs are more or less completely surrounded by coverings of cartilage, the olfactory, optic, and otic (auditory) capsules. With the exception of the optic capsules, these cartilages also eventually fuse with the paired cartilages previously mentioned. In many vertebrates, an additional pair of cartilages, the sphenolaterals (Fig. 192), may be distinguished. These are lateral and somewhat dorsal to the trabeculae, and anterior to the basal plate. These also fuse with the other units, and as a result a single cartilage is formed, having the beginning of side walls. The upward growth (Fig. 193) of these walls continues and eventually is

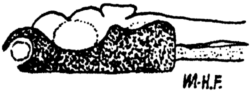


Fig. 193. Up-growth stage of skull development, as seen from the side. (Redrawn from Walter, *Biology of the Vertebrates*, after Roule, by permission of The Macmillan Company, publishers.)

directed medially from both sides, resulting in the formation of a thin roof covering the brain.

It will be noted that the skull at this stage of its development consists entirely of cartilage. It is known as a chondrocranium, and is represented by the adult skull of the elasmobranchs (Fig. 196).

Further development, in all other vertebrates, includes the formation of separate bones arising from definite centers of ossification in the chondrocranium, and the addition of numerous membrane (dermal) bones which have developed in the integument (dermis). The skull of a higher vertebrate thus consists of a series of bones, some of which are of dermal origin, while others are preformed in the cartilage (Fig. 194). The two types cannot be distinguished without knowing their individual history.

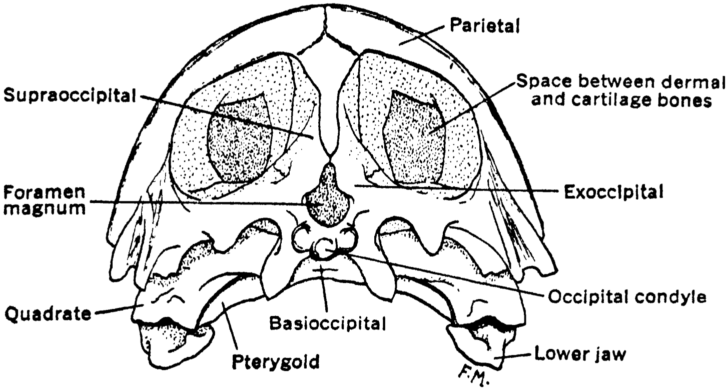


Fig. 194. The turtle skull. Posterior view showing space between dermal and cartilage bones.

Figure 195 shows, very diagrammatically, the various bones in the skull of a typical mammal. The accompanying table (page 184) shows which bones are cartilage bones and which are of dermal origin. If the figure and table are fully understood, the following discussion of the comparative anatomy of the skull should not be found difficult. It should be noted in advance that the skulls of some of the lower vertebrates, particularly the fishes and reptiles, contain more separate bones than do the skulls of mammals. In

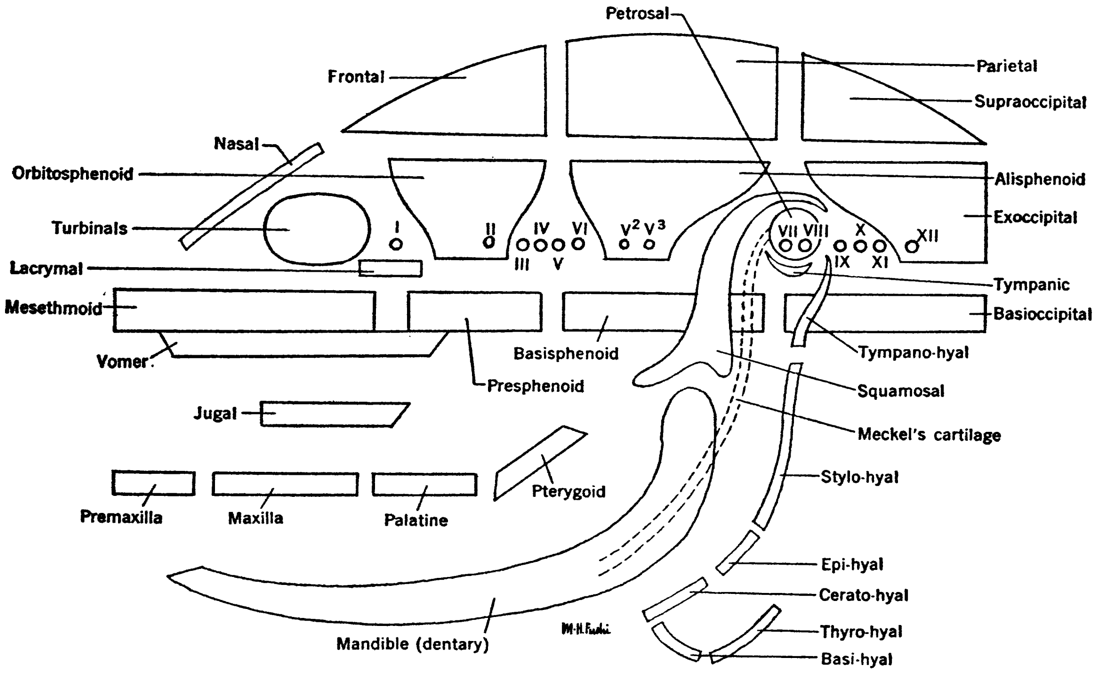


Fig. 195. Diagram showing the relations of the principal bones of the mammalian skull. The Roman numerals indicate the foramina for the corresponding cranial nerves. (Redrawn from Flower, *Osteology of the Mammalia*, by permission of The Macmillan Company, publishers.)

some cases this reduction is due to fusion of bones which were formerly separate; in other cases a given bone has been definitely lost.

A LIST OF THE CHIEF BONES OF THE SKULL

Region	*Dermal*	*Cartilage*	*Single or Paired*
Nasal	Nasal		Paired
	Lacrimal		Paired
		Mesethmoid	Single
		Ectethmoid	Paired
Eye (orbit)	Frontal		Paired
	Prefrontal		Paired
	Postfrontal		Paired
		Presphenoid	Single
		Orbitosphenoid	Paired
		Sclerotics	Several
Ear	Parietal		Paired
	Sphenotic		Paired
	Pterotic		Paired
	Squamosal		Paired
		Basisphenoid	Single
		Alisphenoid	Paired
		Prootic	Paired
		Opisthotic	Paired
		Epiotic	Paired
Roof of mouth	Parasphenoid (vomer)		Single
	Palatine		Paired
	Pterygoid		Paired
	Ectopterygoid		Paired
Cheek	Jugal		Paired
	Quadratojugal		Paired
Posterior cranial	Supraoccipital (interparietal)		Single
		Supraoccipital	Single
		Basioccipital	Single
		Exoccipital	Paired
Upper jaw	Premaxillary		Paired
	Maxillary		Paired
		Quadrate	Paired

Region	*Dermal*	*Cartilage*	*Single or Paired*
Lower jaw	Dentary		Paired
	Splenial		Paired
	Angular		Paired
	Coronoid		Paired
	Surangular		Paired
		Articular	Paired
		Mentomeckelian	Paired
Hyoid		Hyomandibula	Paired
		Symplectic	Paired
		Stylohyal	Paired
		Epihyal	Paired
		Ceratohyal	Paired
		Basihyal	Single
Branchial	Opercular		Paired
	Preopercular		Paired
	Subopercular		Paired
	Interopercular		Paired
		* Pharyngobranchial	Paired
		Epibranchial	Paired
		Ceratobranchial	Paired
		Hypobranchial	Paired
		Basibranchial	Single

---

* Present in typical teleost fishes. Above them varying parts remain and, in association with parts of the hyoid arch, form the hyoid apparatus.

Comparative Anatomy of the Skull

Cyclostomes. As previously stated, very few elements of the skull of the adult cyclostome can be homologized with those of other vertebrates. During development, however, trabeculae, parachordals, and otic capsules may be distinguished. The annular, lingual, anterior, and posterior dorsal cartilages, apparently, are without homologues in higher forms.

Elasmobranchs. In the description of the development of the skull, it was said that the cranium of the elasmobranch (Fig. 196) is a continuous cartilage. The cartilage is penetrated by several large openings, fontanelles, and smaller foramina for the passage of nerves and blood vessels. Although there is much variation in the different members of the group, a number of characteristic features are quite constant. Among these may be mentioned the rostrum, a large anterior projection; the anterior fontanelle, a wide opening into the anterior part of the cranial cavity; and the endolymphatic fossa, a large median depression on the dorsal surface toward the posterior end. The orbits are large lateral cavities in which the eyeball is located. The optic pedicel is a mushroom-shaped cartilage, projecting into the orbit and supporting the eyeball. At the posterior end of the cranium is a large median opening, the foramen magnum, for the exit of the nerve cord. This is bounded laterally by large foramina for the passage of the ninth and tenth cranial nerves.

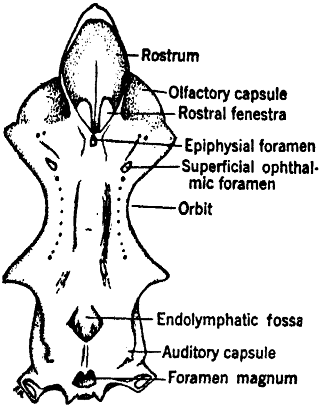


Fig. 196. The skull of *Squalus acanthias*, dorsal view.

Teleostomous fishes. In the Teleostomi, the skull consists of a combination of membrane (dermal) and cartilage bones. In the Chondrostei, there are few cartilage bones, the most important being the orbitosphenoid and alisphenoid. The addition of the numerous dermal bones of the roof of the skull is the most notable advance over the elasmobranch condition. Among the bones characteristic of the higher vertebrates and seen here for the first time are the nasals, parietals, frontals, postfrontals,

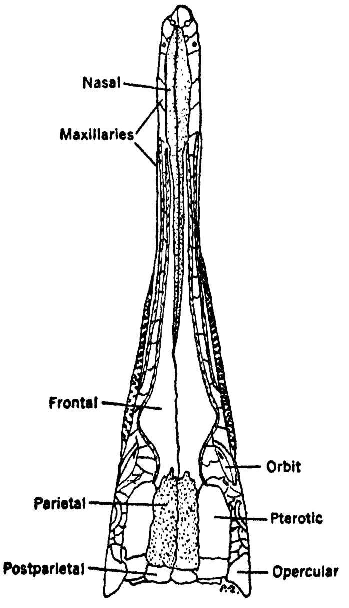


Fig. 197. Skull of *Lepidosteus sp.*, a garpike.

postorbitals, squamosals, and the dermal portion of the supraoccipital.

In the Holostei (Fig. 197), the bones of the skull are similar to those of the lower teleosts. The absence of a supraoccipital in *Amia* (Fig. 198) distinguishes it from other fishes.

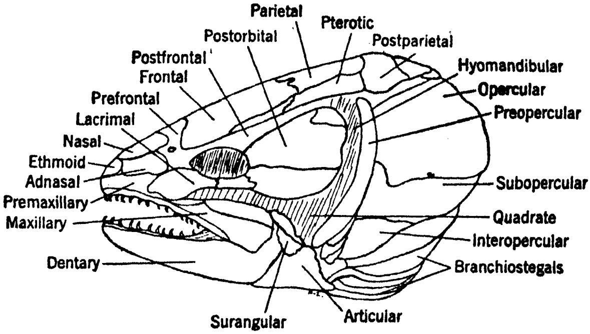


Fig. 198. The skull of *Amia*, lateral view.

In the great group of teleost fishes there is naturally much variation in the size and shape of the skull. Ossification at the base of the cranium gives rise to the supraoccipital, the exoccipital, and the basioccipital bones, which surround the foramen magnum. A large number of separate bones develop in and around the otic capsules, such as proötic, epiotic, sphenotic, and opisthotic. A series of orbitals, supraorbital, preorbital, postorbital, and infraorbital, develop around the eye. The dermal roofing bones previously mentioned are also developed in this group.

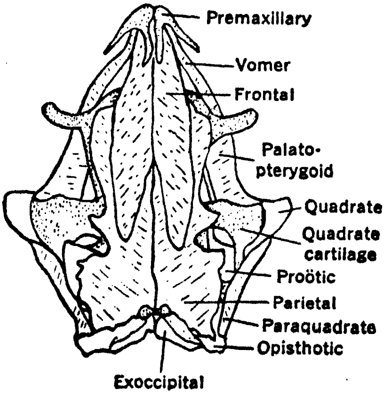


Fig. 199. Dorsal view of skull of *Necturus.* (Redrawn from Walter, *Biology of the Vertebrates*, after Wilder, by permission of The Macmillan Company, publishers.)

In the Dipnoi there is little ossification in the adult skull. A pair of exoccipitals is present. The membrane bones also are not as numerous as in other fishes. A median nasal is described, also a long and slender bone known as the frontoparietal.

Amphibians. The amphibian neurocranium consists largely of membrane bones and cartilage. With the exception of the Gymnophiona, the cranium is broad and flat (Fig. 199). Like that of other tetrapods, it is movable on the vertebral column, having surfaces (occipital condyles) for articulation with the first cervical vertebra. In this group there are two condyles, located on the exoccipital bones at the sides of the foramen magnum. Ossified basioccipitals and supraoccipitals are not present. The skull of the Caudata is more degenerate than that of the other amphibians, having a small number of cartilage and dermal bones. The proötic is the only ossification in the otic capsule. In the interorbital region, there are paired orbitosphenoids. The roofing bones of the cranium include the parietal, the frontal, the nasal, and sometimes, the lacrimal. The middle of the roof of the mouth contains a large bone, the parasphenoid.

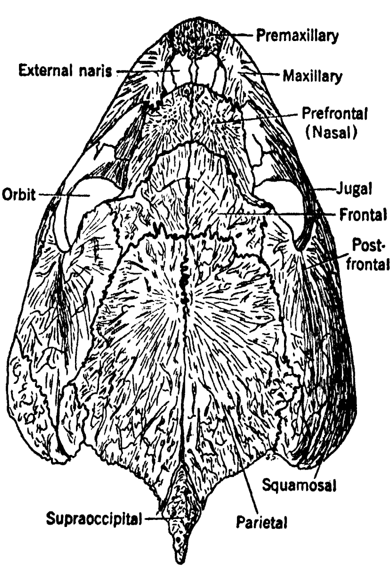


Fig. 200. The skull of a turtle, dorsal view.

In the Salientia a large part of the chondrocranium is retained. The cartilage bones of the adult include the paired exoccipitals, proötics, and ethmoids. The dermal bones, frontal and parietal, are fused, forming the frontoparietal. Nasals and squamosals are present.

Reptiles. A large number of bones are present in the reptile skull (Fig. 200). The roof consists of the usual membrane bones, nasal (lacking in most turtles), lacrimal, frontal, prefrontal, postfrontal, parietal, and squamosal. The turtle skull is completely roofed over, but in many reptiles there are large openings in the temporal region. In the crocodilians (Fig. 201) there are two of these, the superior and inferior temporal fossae. These are separated from the orbit by the postorbital bar, usually formed by postorbital and postfrontal bones. In other reptiles, there is a single temporal fossa on each side, while in the snakes (Fig. 202) this also has disappeared. The four occipitals are present with a single (median) occipital condyle. This may be tripartite as in many turtles, the exoccipitals contributing to its formation (Fig. 194). *Sphenodon* (Fig. 203) and most lizards have a parietal foramen for the pineal eye between the two parietals. In addition to the occipitals, among the cartilage bones present are the basisphenoid and alisphenoid.

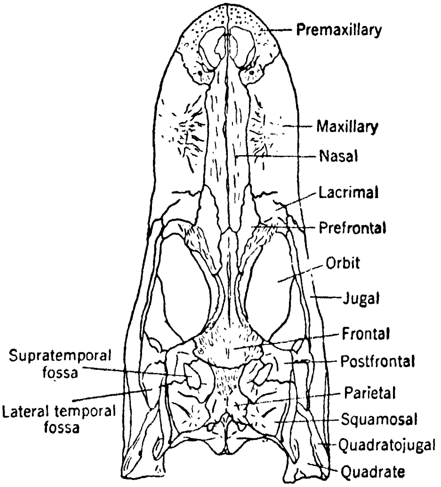


Fig. 201. The skull of *Alligator*, dorsal view.

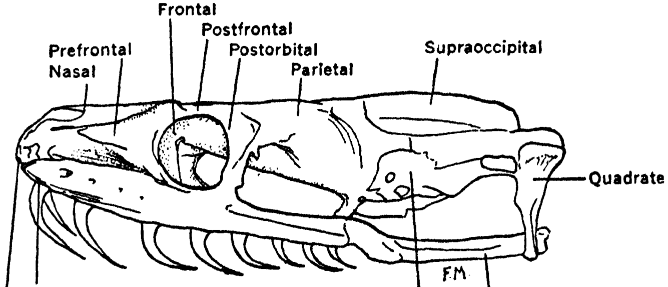


Fig. 202. Skull of a python.

Birds. The avian skull (Fig. 204) is similar to that of the reptiles in many respects. There is a single occipital condyle (basioccipital). Because of the greater development of the brain, the cranial cavity is much larger than in the preceding classes. Because of the flexures or bendings of the brain and the more vertical position of the neck, the skull is carried at nearly a right angle to the axis of the body. Many of the separate bones characteristic of the reptilian skull have apparently been lost. This is probably due in many cases to the fusion of adjoining bones to form bone complexes. The orbit is large and is continuous with the single temporal fossa. In the adult skull, replacement of cartilage is almost complete, and both dermal and cartilage bones are so completely

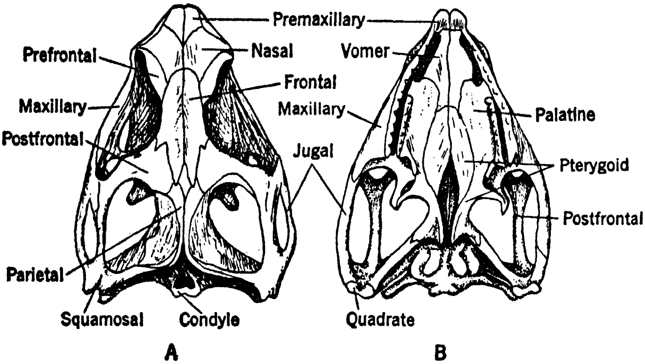


Fig. 203. The skull of *Sphenodon.* A, dorsal view; B, ventral view. (Redrawn from Parker and Haswell, after the *Cambridge Natural History*, by permission of The Macmillan Company, publishers.)

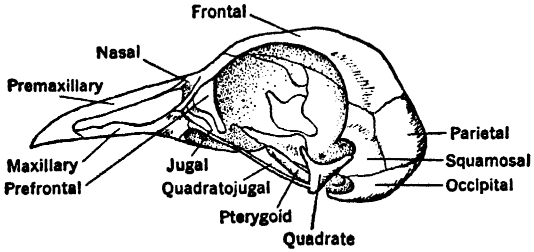


Fig. 204. The skull of the pigeon, lateral view. (Redrawn from De Beer, *Vertebrate Zoölogy*, by permission of The Macmillan Company, publishers.)

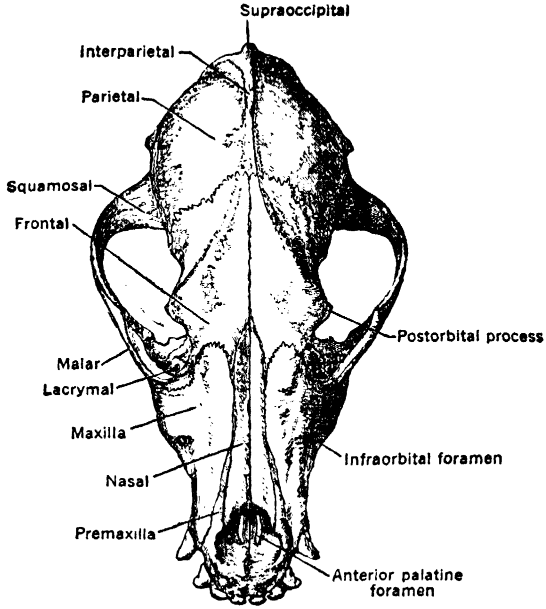


Fig. 205. Dorsal surface of the skull of a dog. (From Flower, *Osteology of the Mammalia*, by permission of Macmillan & Co., publishers.)

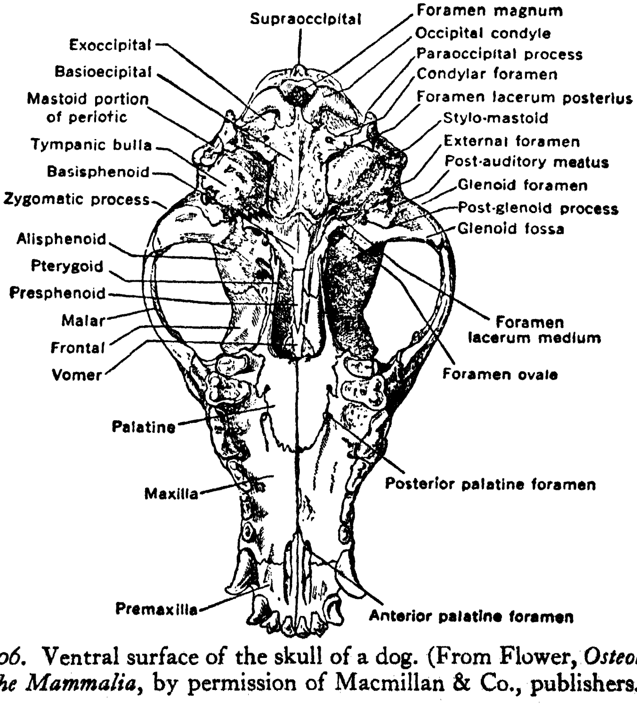


Fig. 206. Ventral surface of the skull of a dog. (From Flower, *Osteology of the Mammalia*, by permission of Macmillan & Co., publishers.)

fused that the usual sutures are obliterated. Many of the bones are exceedingly thin and light.

Mammals. The great size of the mammalian brain has been an important factor in determining the shape of the mammalian skull. In general, there has been an expansion dorsally (Fig. 207) and laterally of the walls of the cranium. There are two occipital condyles (Fig. 208). The foramen magnum is on the ventral surface of the skull in the higher primates. The number of bones is less than in the preceding classes (Fig. 209). This condition is due partly to a loss of bones, and partly to a fusion of those remaining. Among the bones lost are the prefrontal and postfrontal, and the postorbital. The members of the otic series have fused to form the petrosal, which often unites with the squamosal and tympanic, forming the temporal. The sphenoid bones unite to form a single sphenoid, or sometimes two bones, the orbitosphenoid and alisphenoid. The four occipitals typically fuse, forming the

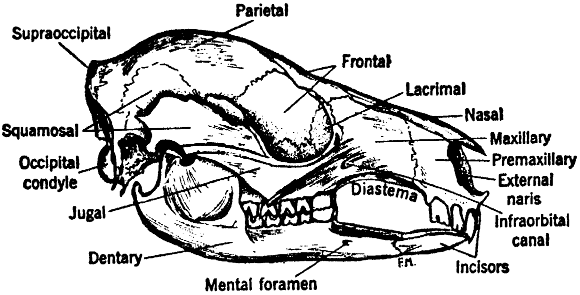


Fig. 207. The skull of a kangaroo, lateral view.

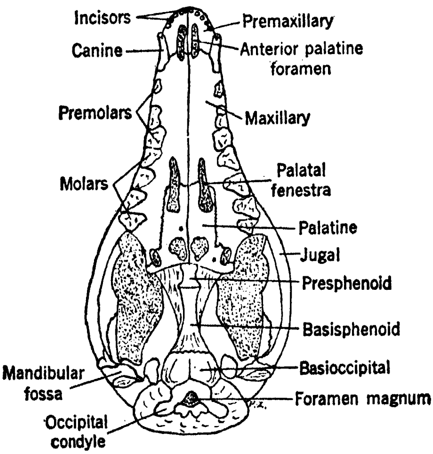


Fig. 208. The skull of the opossum, ventral view.

occipital complex. The number of cartilage bones is greater than in modern reptiles.

The dorsal roof (Fig. 210) of the mammalian neurocranium consists of the following membrane bones — the nasal, lacrimal, frontal, parietal, and a portion of the supraoccipital (Fig. 211). The ventral portion of the neurocranium contains such cartilage bones as mesethmoid, presphenoid, basisphenoid, and basioccipital. Between these two groups are the more or less vertically arranged cartilage bones, orbitosphenoid, alisphenoid, exoccipital, and the rest of the supraoccipital. In the nasal cavity are the turbinals, formed by ossification of parts of the nasal capsules.

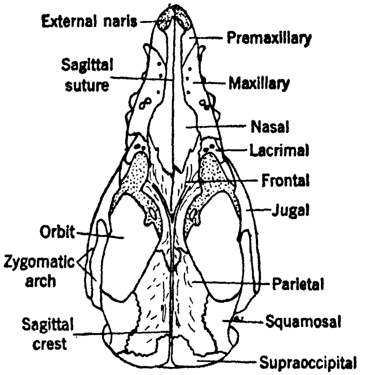


Fig. 209. The skull of the opossum, dorsal view.

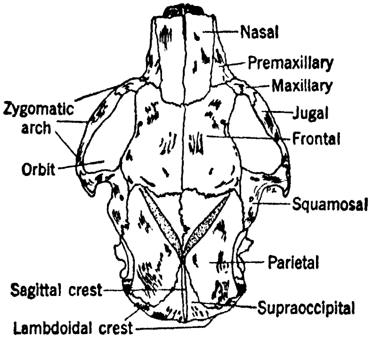


Fig. 210. The skull of the porcupine, dorsal view.

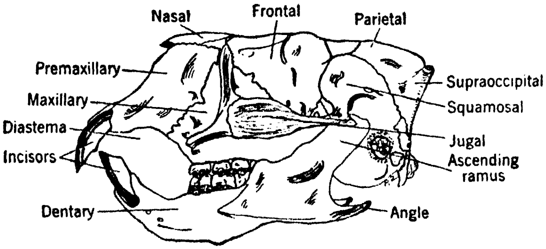


Fig. 211. The skull of the porcupine, lateral view.

A longitudinal section of the mammalian skull (Fig. 212) shows the large size of the brain which would fill a greater part of the cerebral and cerebellar fossae. The sella turcica is a small depression in which the pituitary body lies.

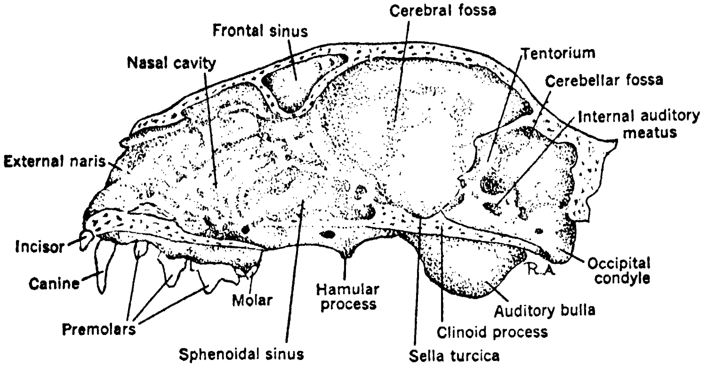


Fig. 212. Longitudinal section of the cat skull.

The Visceral Arches

The visceral skeleton, or splanchnocranium, includes that part of the skeleton surrounding the anterior part of the alimentary canal. It consists primarily of a series of cartilaginous arches which develop in relation to the respiratory structures of aquatic animals. Many of those elements have a most interesting history (see table on page 195). In terrestrial forms parts freed from their relation to the gills perform a variety of other functions. Some become the auditory ossicles of mammals; others form the hyoid bones supporting the tongue; while remains of still others may be seen in the various cartilages of the mammalian larynx.

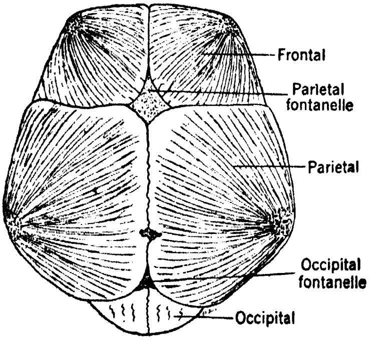


Fig. 213. The skull of the human infant, dorsal view, showing fontanelles.

The visceral skeleton of a typical elasmobranch (*Squalus*) may be taken as the starting point, since it is practically im-

PHYLOGENY OF THE VISCERAL ARCHES (Not including dermal bones)

Number of Arch	*Chondrichthyes*	*Osteichthyes*	*Amphibia*	*Reptilia and Aves*	*Mammalia*
1st Visceral (Mandibular)	Palatoquadrate (Upper jaw)	Quadrate	Quadrate	Quadrate	Incus
	Meckel's (Lower jaw)	Articular	Articular	Articular	Malleus
2nd Visceral (Hyoid)	Hyomandibulars	Hyomandibula	Columella	Stapes	Stapes
	Ceratohyals Basihyal	Hyoid apparatus	Hyoid apparatus	Hyoid apparatus	Styloid process Pinna cartilages Hyoid apparatus
3d Visceral (1st Branchial)	Each arch may contain the following cartilages: Pharyngobranchial Epibranchial Ceratobranchial Hypobranchial Basibranchial. The first four are paired, the last is median and ventral. The first three are the most constant, the other two often fusing in adjoining segments.	The same paired and median elements may be present. They are generally ossified. They are subject to much modification and reduction, in the different species, especially in the case of the more posterior arches.	Many of the same parts, more or less ossified, are present in the larval stages. In the adult variable parts remain and are closely associated with the hyoid apparatus in the form of cornua or processes.	Several slender cornua are present in lizards and turtles, representing the 1st and 2nd branchial arches. These are still further reduced in the birds.	Posterior cornua of the hyoid apparatus
4th Visceral (2nd Branchial)					? ? ?
5th Visceral (3d Branchial)					? ? ?
6th Visceral (4th Branchial)					Cartilage of epiglottis (?) Part of thyroid cartilage of larynx
7th Visceral (5th Branchial)			Lateral, cricoid, and arytenoid cartilages of larynx Tracheal rings	Cricoid and arytenoid cartilages of larynx Tracheal rings	Part of thyroid cartilage of larynx Arytenoid and cricoid cartilages and the tracheal rings

possible to find homologous structures in the cyclostomes. In the spiny dogfish (*Squalus acanthias*) the visceral skeleton consists of seven arches. The first of these, the mandibular, consists of two pairs of cartilages, the anterior palatoquadrates and the posterior Meckel's. Between these two paired cartilages is the mouth opening. The second visceral arch, known as the hyoid, consists of a pair of dorsal cartilages, the hyomandibulars, paired lateral ceratohyals, and a median ventral basihyal. Posterior to the hyoid arch is a series of five branchial arches. A complete branchial arch consists of four paired cartilages, which are in order, beginning dorsally, the pharyngobranchials, epibranchials, ceratobranchials, and hypobranchials, and a median ventral cartilage, the basibranchial. The first and fifth arches are not complete in *Squalus*, being without hypobranchials, while there are only two basibranchials. The anterior basibranchial is small, while the posterior one is a broad flattened plate.

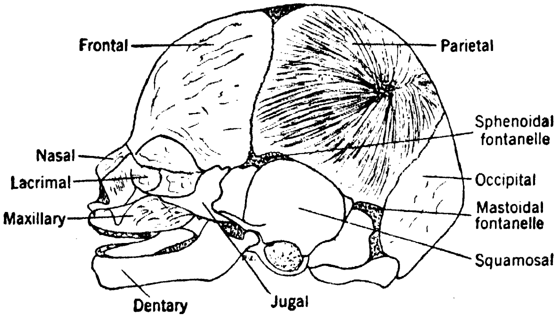


Fig. 214. The skull of the human infant, lateral view.

The first, or mandibular, arch forms the upper (palatoquadrate) and lower (Meckel's) jaw. The hyoid arch aids in supporting the floor of the mouth and in many cases plays a part in the suspension of the jaws. The branchial arches support the gills.

In vertebrates above the elasmobranchs, many investing (dermal) and replacing (cartilage) bones are added to parts of the visceral skeleton, particularly to the mandibular arch. For example, such dermal bones as the premaxillary, maxillary, vomer, pterygoid, and palatine develop around the pterygoquadrate to form the upper jaw and the roof of the mouth. The posterior part of the pterygoquadrate ossifies, giving rise to the quadrate with which the lower jaw articulates in all vertebrates below the mammals. Dermal bones associated with Meckel's cartilages are the dentary, angular, surangular, and splenial (Fig. 215). The most important

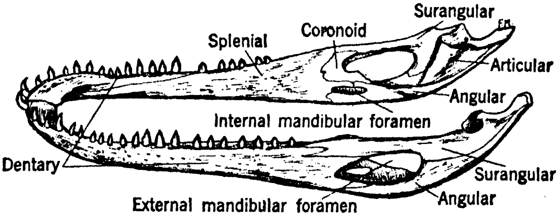


Fig. 215. The lower jaw of the alligator, showing the large number of bones characteristic of the reptiles.

ossification gives rise to the articular, which forms the articulation with the quadrate (mammals excepted). In the mammals the lower jaw consists of a single bone, the dentary (Fig. 216), which articulates with the squamosal. It has been satisfactorily determined that the articular and quadrate, losing their former function of jaw suspension, have in the mammals moved into the middle ear as the malleus and incus, respectively.

The history of the hyoid arch shows less bone formation. The part played by the hyomandibular in connection with jaw suspension in the Chondrichthyes has been described. In the bony fishes the dorsal part of this cartilage ossifies to form a bone, the hyomandibula. In vertebrates above the fishes the hyomandibular, or at least a part of it, contributes to the formation of the columella auris, a bone or series of bones associated with the middle ear.

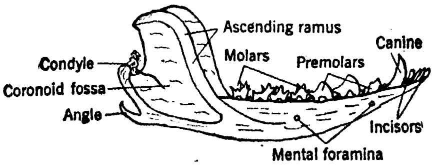


Fig. 216. The lower jaw (dentary bone) of the opossum.

In the amphibians the columella auris usually consists of two parts which may not be completely ossified. One of these, the plectrum, touches the tympanic membrane; the other, known as the operculum, fits into the oval window. In *Necturus* these parts are united.

In the reptiles the columella auris consists of two parts, the stapes which fits into the oval window and an extrastapedial cartilage (extracolumella) in contact with the eardrum. Any homology between these parts and the similar structures in amphibians has not been determined.

The columella auris of birds is similar to that of the reptiles except for the shape of the various parts of the extrastapes.

In the mammals it is quite generally agreed that the stapes is a derivative of a part of the hyomandibular. The phylogeny of the other bones of the mammalian ear, the malleus and the incus, has been mentioned above. One end of the malleus is attached to the inner surface of the tympanic membrane. The inner and broad surface of the stapes fits into the oval window. The incus completes the chain by forming the connection between malleus and stapes.

The remaining portion of the hyoid arch in land vertebrates becomes very much modified to form the hyoid apparatus which supports the tongue and the larynx and also serves as a place of attachment for numerous muscles.

In the amphibians the hyoid arch is also associated with respiratory movements of the floor of the mouth. In the frog it consists of a broad plate, the body of the hyoid, attached to which are four paired processes. The anterior of these are attached to the proötic bones of the skull. The two posterior processes, the thyrohyals, are more or less ossified and extend to the larynx which they help to support.

In reptiles the branchial arches are associated with the hyoid in the formation of the hyoid apparatus. In the alligator, the hyoid consists of a broad cartilaginous body and a pair of horns which extend from it, posteriorly and dorsally.

In the mammals the hyoid consists of a narrow bone, the body or basihyal, located in front of the larynx; and two pairs of horns (cornua), each of which consists of several short rodlike bones. In the cat each anterior horn consists of four separate pieces which are, beginning at the body: the hypohyal, ceratohyal, stylohyal, and tympanohyal. The latter articulates with the auditory bulla near the stylomastoid foramen. The posterior horns consist of a single piece, the thyrohyal, which is attached to the larynx.

The human hyoid is a horseshoe-shaped bone which consists of a central portion, the body, with two projecting horns, the greater and lesser cornua, on each side. It is located just anterior to the larynx and is suspended from the styloid processes of the temporal bones of the skull. It supports the tongue and is the place of attachment for many muscles.

The remaining parts of the visceral skeleton are the branchial arches, which were described in detail as they are seen in the spiny dogfish. In the bony fishes those which remain are generally ossified. In the larval and permanently aquatic amphibians, the branchials are more or less fishlike. In the adult anurans the remaining branchials are associated with the hyoid apparatus. The relations are somewhat similar in the land vertebrates where these arches serve no longer for respiratory purposes. Some of them remain as parts of the processes or cornua of the hyoid apparatus; others give rise to the cartilages of the larynx. These latter will be considered in a subsequent chapter in a discussion of the phylogeny of the larynx.

It was stated above that parts of the splanchnocranium become firmly united with the neurocranium to form the skull of the adult. The upper jaw becomes more and more firmly united with the floor of the neurocranium, while the lower jaw is attached to the upper in a variety of ways (Fig. 217). The phylogeny of jaw suspension still presents a rather confusing picture.

In primitive elasmobranchs the hyoid arch contributes to the suspension of both upper and lower jaws which are attached to it by ligaments. It is, in turn, attached by ligaments to the otic capsule. The palatoquadrate may also be suspended from the floor of the chondrocranium by ligaments. This type of suspension is called amphistylic.

In the Holocephali the palatoquadrate is entirely fused to the chondrocranium and the lower jaw articulates with the posterior (quadrate) portion of it. This is called the holostylic method.

The socalled hyostylic method is characteristic of most modern elasmobranchs. In these forms the hyomandibular is attached to the otic capsule and both jaws are suspended from it by ligaments.

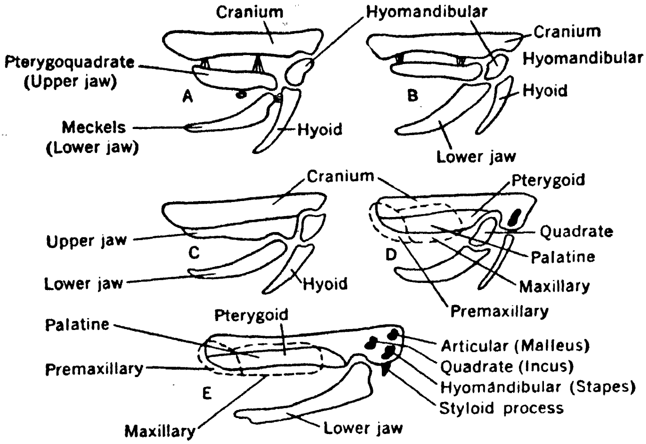


Fig. 217. Diagrams of different methods of suspension for the lower jaw. A, hyostylic (elasmobranchs); B, amphistylic (*Notidanus*, a primitive shark); C, holostylic (holocephalans); D, autostylic (many dipnoans, ganoids, teleosts, amphibians, reptiles, and birds); E, craniostylic (mammals). (Redrawn from Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

In most vertebrates the hyoid arch does not take part in jaw suspension. The palatoquadrate articulates with, or is fused to, the floor of the cranium. The lower jaw articulates with the posterior portion of the bone (quadrate) which forms in it. This is the autostylic method.

In mammals, as we have seen, there is an entirely new method of suspension of the lower jaw. In this class the lower jaw is attached directly to the squamosal bone. The bones of the upper jaw are inseparably united with the cranial portion of the skull. This type may be called craniostylic.

The Appendicular Skeleton

The appendicular skeleton includes the parts of the pectoral and pelvic girdles and of the appendages. Two types of appendages are present in the vertebrates, the median and the paired. The former are confined to the cyclostomes, fishes, and members of higher groups that have returned to an aquatic environment. Paired appendages are characteristic of all classes above the cyclostomes, although there are numerous exceptional forms in which one or both pairs of limbs have been reduced or lost.

THE MEDIAN FINS. The median appendages of a typical fish are four in number, two dorsal, one caudal, and one ventral fin. The dorsal and ventral fins are supported by a series of parallel cartilaginous or bony rods, the pterygiophores. These rods may be divided into two or three elements. The paired dermal rays lie distal to the terminal elements of these rods, and in some forms embrace them. In the caudal fins, if pterygiophores are absent, the dermal rays are supported by the spinous processes of the vertebrae.

Four types of caudal fins (tails) are recognized (Fig. 35). The distinction is based upon the degree of symmetry, both internal and external, that exists between dorsal and ventral portions of the fin.

In the protocercal type, which is considered primitive, the fin is equally developed above and below the vertebral axis. This results in external and internal symmetry. It is characteristic of cyclostomes and of the embryo of most fishes.

The heterocercal type, which is characteristic of elasmobranch fishes, is asymmetrical both internally and externally. The ventral lobe of the fin is much longer than the dorsal portion. The end of the vertebral column extends into the dorsal lobe. The haemal arches are much larger than the neurals.

The name diphycercal is applied to those caudal fins that have become secondarily symmetrical, both internally and externally. Such fins are the result of modification of the heterocercal type. They cannot be distinguished from the protocercal type with which they are often confused. They are found in some of the crossopterygians.

In most higher fishes the tail is said to be homocercal. This type is symmetrical externally but not internally. The end of the vertebral column is turned upward into the dorsal part of the fin. The last centrum, or several centra fused, forms a long bone, the urostyle, which points upward. The last few haemal arches are enlarged. Such fins are derived embryologically from the heterocercal type.

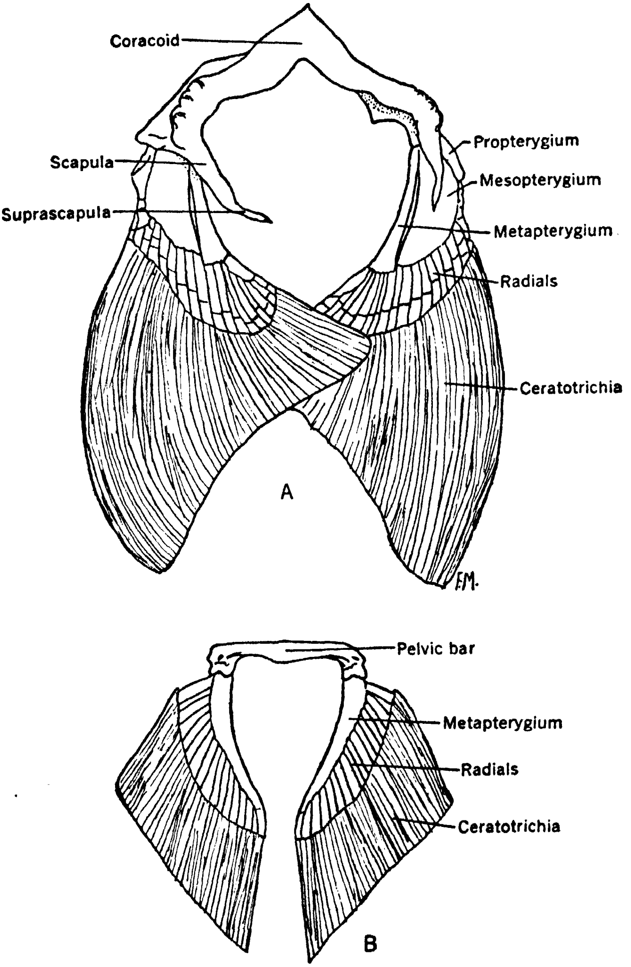


Fig. 218. The appendicular skeleton of *Squalus acanthias.* A, pectoral girdle and fin; B, pelvic girdle and fin.

THE PAIRED APPENDAGES. In practically all vertebrates the skeleton of the paired appendages becomes differentiated into a supporting girdle and a series of bones extending into the free part of the limbs. The typical location of the pectoral girdle is near the heart, and that of the pelvic girdle in the vicinity of the anus. In some of the higher fishes, the pelvic fins have migrated anteriorly to take a position ventral to the pectoral fins or even anterior to them.

The girdles. The pectoral girdle seen in a primitive condition, as in the common elasmobranchs (Fig. 218), consists of a continuous U-shaped cartilage lying just posterior to the gill region. The ventral part of this cartilage is the coracoid portion; the sides of the U which extend dorsally are the scapular regions. Between coracoid and scapular regions is the glenoid surface where the articulation of the cartilages of the fin takes place. In the higher vertebrates several bones (Fig. 219) are formed in both halves of the girdle by ossification within the cartilage. Among these are the scapula, suprascapula, precoracoid, and coracoid. Membrane bones also are added to the girdle. Among these are the clavicle, cleithrum, supracleithrum, and posttemporal in fishes, and the interclavicle and clavicle of higher forms. The posttemporal serves to attach the pectoral girdle to the skull. There is a reduction and a loss of many of these dermal bones in the tetrapods. The cleithrum is not present in any living form above the fishes. Both interclavicle and clavicle remain in reptiles and birds. Among the mammals the interclavicle is found in monotremes only. The clavicle is reduced

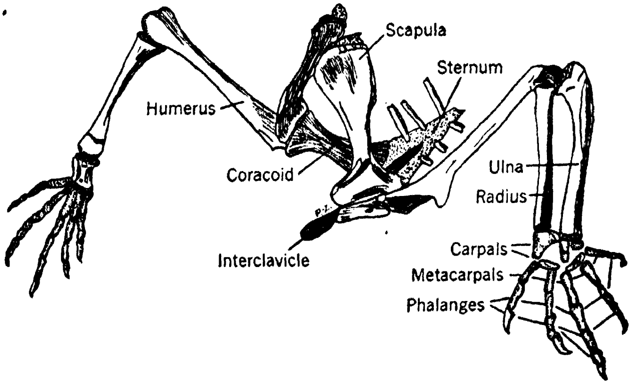


Fig. 219. The pectoral girdle and fore limb of the alligator.

in many mammals (carnivores) and is lost in others (ungulates). It is a large and strong bone in the primates and rodents, where it forms a brace between the scapula and the sternum.

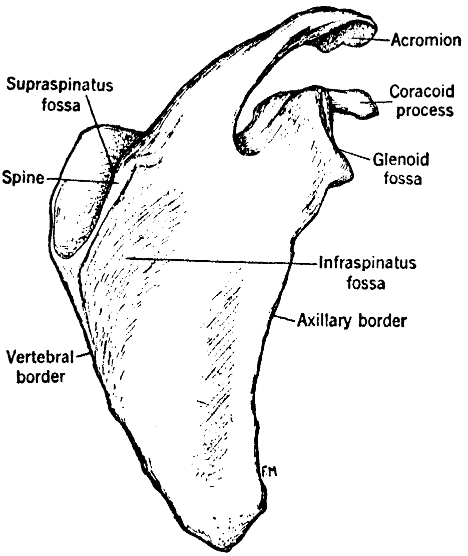


Fig. 220. The human scapula.

The most important cartilage bones of the pectoral girdle have been mentioned above. In some of the Osteichthyes there are two separate bones, the scapula and the coracoid. In others this region may remain as a single cartilage, partly divisible into scapula and coracoid portions.

In the urodeles the pectoral girdle is not fully ossified. The coracoid is a flat cartilaginous plate located ventrally. The dorsal scapula is more fully ossified except for the suprascapular cartilage continuous with its dorsal border. In the anurans the girdle is more fully ossified, consisting ventrally of an anterior rodlike clavicle and a posterior coracoid.

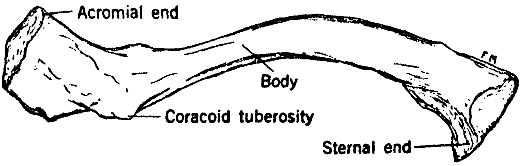


Fig. 221. The human clavicle.

Beneath the clavicle is the cartilaginous precoracoid. The dorsal part of each girdle consists of a bony scapula and a cartilaginous suprascapula extending dorsally from it.

There is considerable variation in the parts of the pectoral girdle among the reptiles. In *Sphenodon* there is a precoracoid and scapula on either side, the latter bearing a suprascapular cartilage. The dermal bones present are a pair of slender clavicles and a median T-shaped interclavicle. The pectoral girdle of lizards is quite similar. In the alligator clavicles are missing.

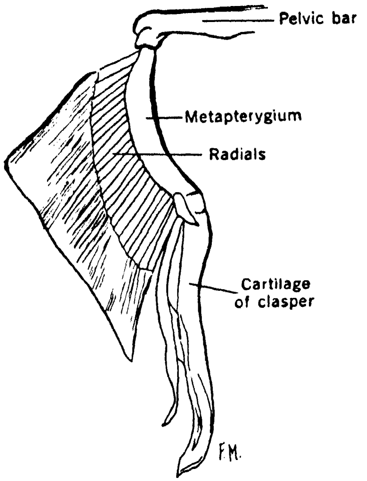


Fig. 222. The pelvic girdle and fin of the male dogfish, *Squalus acanthias.*

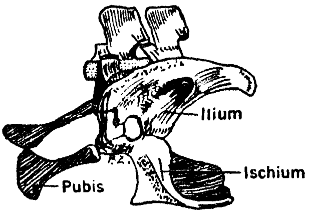


Fig. 223. The pelvic girdle of the alligator.

In the birds the pectoral girdle consists of the scapulae, long thin bones above the ribs; the coracoids, heavier bones which reach to the sternum; and the anterior and ventral wishbone. The latter includes the clavicles and the interclavicle.

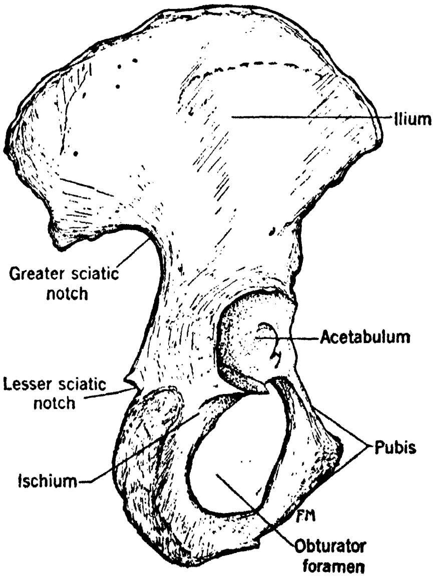


Fig. 224. The human pelvic girdle.

The pectoral girdle of the placental mammals consists chiefly of the scapula (Fig. 220), with which the coracoid has united, forming the coracoid process. A separate coracoid is present in mammals in the monotremes only. The clavicles are reduced or lost in ungulates, the Cetacea and the Sirenia. In man (Fig. 221), they are well developed, forming a brace between scapula and sternum.

The pelvic girdle (Fig. 222) of the elasmobranchs usually consists of a single bar of cartilage. In higher vertebrates (Fig. 223), three cartilage bones develop in either half of the girdle. These are the ilium dorsally (and anteriorly), the ischium posteriorly, and the pubis ventrally. A cuplike depression, the acetabulum, in the formation of which these three bones participate, forms the articulation for the long bones of the limbs. A large opening, the obturator foramen, between the ischium and pubis is typical of many vertebrates (Fig. 224). The two halves of the girdle often meet ventrally in the median plane at the pubic or ischiac symphysis. The three bones of each side unite early in the birds and mammals (monotremes excepted), forming the so-called innominate bone (Fig. 225). In the monotremes and marsupials an additional bone, the prepubis (Fig. 226), extends anteriorly and laterally from each pubis. A small additional bone, the acetabular or cotyloid (Fig. 225), is often present within the acetabulum in mammals.

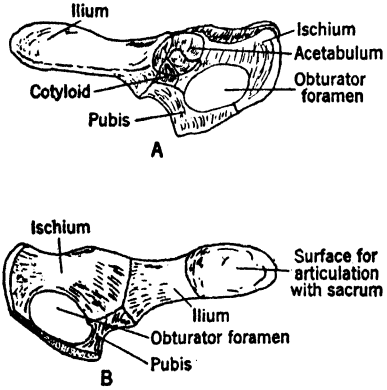


Fig. 225. The pelvic girdle (innominate bone) of a young cat, showing sutures. A, lateral surface; B, medial surface.

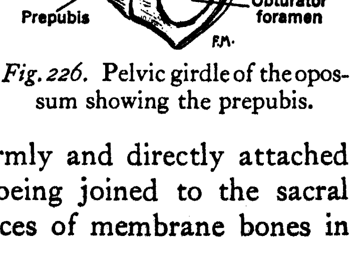


Fig. 226. Pelvic girdle of the opossum showing the prepubis.

In most vertebrates above the fishes, the pelvic girdle is firmly and directly attached to the axial skeleton, the ilia being joined to the sacral vertebrae. There are no evidences of membrane bones in the pelvic girdle.

THE FREE APPENDAGE

Fish type. The skeleton of the pectoral fins of the typical elasmobranchs (Fig. 218) consists proximally of three basal cartilages, articulating with the glenoid surface of the girdle; and distally, of a series of jointed cartilages, the radialia. The basal cartilages are, beginning laterally, the propterygium, the mesopterygium, and the metapterygium. Extending beyond the radials are the dermal rays previously mentioned. In the higher fishes, this same general plan, subject to much variation in details and in the amount of ossification of the various elements, is apparent. In most elasmobranchs there is but a single pair of basal cartilages in the pelvic fin. These correspond to the metapterygium of the pectoral fin. The distal elements, radialia, do not differ greatly from those in the pectoral fin.

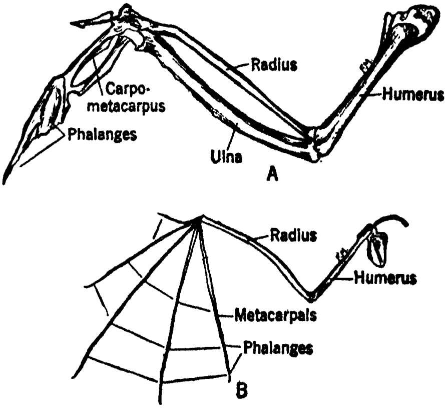


Fig. 227. The skeleton of the fore limb of a bird and bat, showing homologies. A, bird; B, bat.

Tetrapod type. The skeleton of the free limbs of land-living forms differs greatly from that described as characteristic of the fishes. In terrestrial forms the appendages must support the weight of the body. Furthermore, the use of the appendages in locomotion requires a certain amount of flexibility, which is provided by the joints between the various elements (Fig. 227).

The parts of the pectoral and pelvic limbs are so nearly alike that they will be named together, the bone of the pectoral limb, in each case, being named first (Fig. 229). The proximal element is a single bone, the humerus or the femur. The former articulates with the glenoid cavity; the latter, at the acetabulum. Distal to each of these is a pair of bones, the radius and ulna, and the tibia and fibula, respectively.

Each of these bones is subject to so great variation in the different vertebrates, or even between the members of the same class, that a detailed description of them is impossible here. The more general features only will be described. In most cases all of these bones are relatively long and slender as compared with the other parts of the skeleton of a given animal. These so-called long bones will be described briefly before considering the remaining parts of the appendicular skeleton.

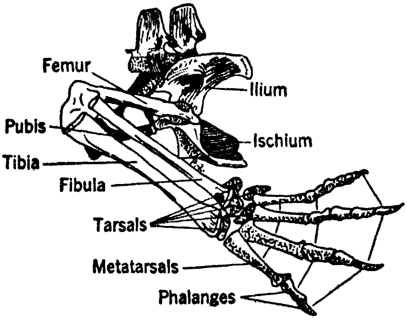


Fig. 228. The pelvic girdle and hind limb of the alligator.

The typical humerus of a mammal has a large rounded head which fits into the glenoid cavity of the scapula. At the sides of the head are two projections, the greater and lesser tuberosities. The deltoid ridge, an elevation or crest on the anterior surface of the shaft, below the tuberosities, is a place of attachment of important muscles. The distal end of the humerus contains surfaces for articulation with the ulna and the radius. The lateral of these, the capitulum, articulates with the radius; the medial surface, or trochlea, with the ulna. At the side and somewhat above these surfaces are rough projections, the medial and lateral epicondyles. The humerus is often perforated by a large foramen, the supracondyloid, near the medial epicondyle. This is not present in man. A large depression on the posterior surface of the distal end is known as the olecranon fossa.

In the birds the humerus is short and strong. The pneumatic foramen is a large opening into the air cavity of the humerus. It is located near the greater tuberosity.

The ulna and radius form the skeleton of the forearm. The radius, which is on the side of the thumb or first digit, is usually shorter and lighter than the ulna. The proximal end of the ulna consists of a large projection, the olecranon process. The semilunar notch, with which the trochlea of the humerus articulates, is a deep cavity distal to the olecranon. Just distal to this notch is a small projection, the coronoid process. The radial notch, which is opposite the coronoid process, is a transverse depression in which the head of the radius may rotate. The ulna bears on its distal end a styloid process. The radius consists of a head at the proximal end; a roughened tuberosity a short distance from the head; a rounded shaft; and a projection, the styloid process, at its distal end.

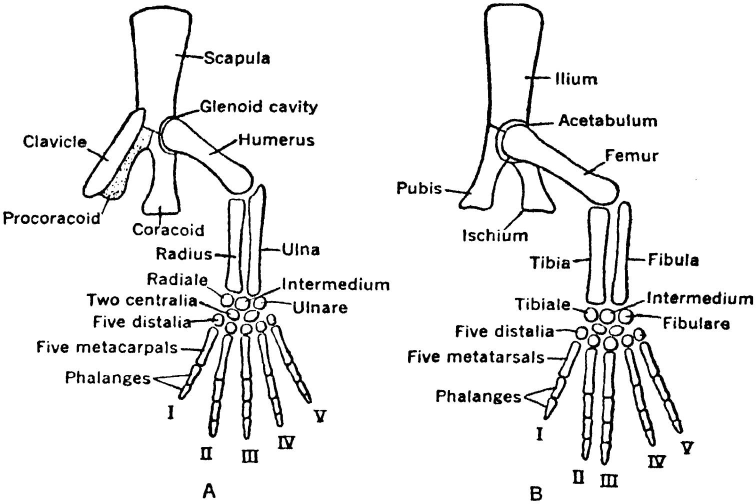


Fig. 229. Diagrams of the plan of the vertebrate limbs. A, pectoral girdle and fore limb; B, pelvic girdle and hind limb. (From Woodruff, *Animal Biology*, after Parker and Haswell, by permission of The Macmillan Company, publishers.)

In the bird the radius and ulna are long and slender. The ulna has an olecranon process. This structure is not present in lower classes.

The radius and ulna are fused in the frog forming the so-called radioulna. There is a tendency in mammals toward a reduction of the ulna as compared to the radius. In others there is a partial fusion of these two bones. In those mammals, particularly the primates, in which the forelimb is used for a variety of movements, there is a great deal of flexibility between the ulna and radius. This may be illustrated by rotating the hand at the wrist, to bring either surface uppermost. During these movements the head of the radius rotates in the radial notch, and the shaft of the radius crosses that of the ulna obliquely. In quadrupedal mammals such a position of the two bones is more or less permanent.

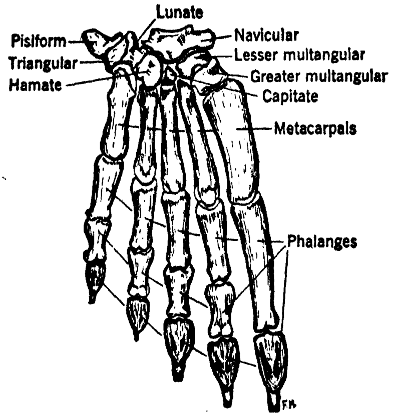


Fig. 230. The fore foot of the seal.

The femur of the hind limb occupies a position corresponding to that of the humerus in the fore limb. It is the only bone of the thigh. A typical femur has a rounded shaft, on the proximal end of which is a projecting head, which fits into the acetabulum of the pelvic girdle. A large projection,

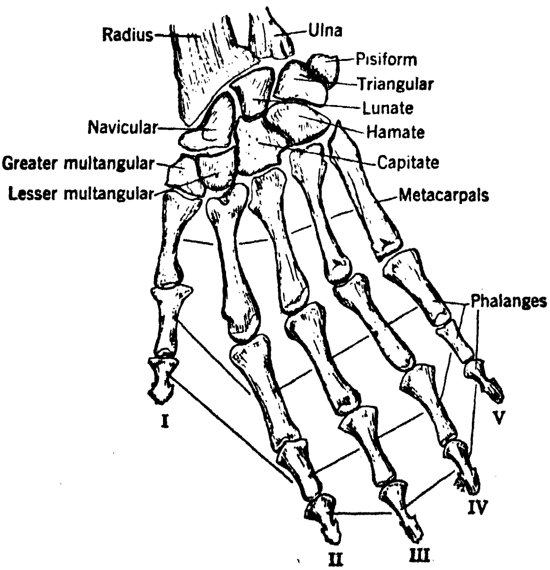


Fig. 231. The bones of the human hand.

lateral to the head, is known as the greater trochanter. A similar and smaller projection distal to the head is the lesser trochanter. The horse and its relatives have a third trochanter. These provide attachment for various muscles. The medial and lateral condyles are articular processes at the distal end, which articulate with the tibia. At the sides of these there are epicondyles. The linea aspera is a long ridge for muscle attachment on the posterior surface of the shaft.

The patella, or kneecap, is an extra bone present in birds and mammals in front of the knee joint. This is attached to the femur by a ligament. It is a sesamoid bone, that is, one that develops within a tendon.

The bones of the shank are the tibia and fibula. The tibia, located medially, is much the larger. It is made up of a long shaft with enlarged proximal and distal ends. The proximal end bears lateral and medial condyles which articulate with the femur. The distal end is much smaller and is prolonged medially into a large projection, the medial malleolus. In the bird the distal end of the tibia is fused to the proximal bones of the ankle to form the tibiotarsus.

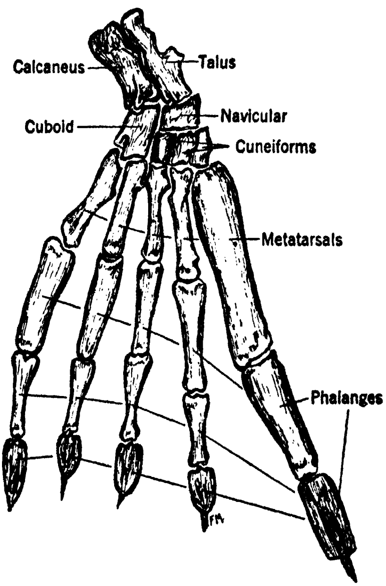


Fig. 232. The hind foot of the seal.

The fibula is always a slender bone, both ends of which articulate chiefly with surfaces on the tibia. The proximal end bears a styloid process; the distal end, a lateral malleolus. In many cases the fibula is either very much reduced or more or less completely fused with the tibia. In the birds its distal portion is lost. In the frog the bones of the shank are fused, forming the tibiofibula.

The remaining bones of the limbs are the carpals (wrist), metacarpals (palm), and phalanges (digits) in the fore foot; and the tarsals (ankle), metatarsals (instep), and phalanges (digits) in the hind foot. Although these bones are subject to much variation in number in different forms, a fairly typical arrangement may be recognized. The carpals usually appear in two definite rows (Fig. 229). The proximal row consists of three bones, the radiale (distal to radius), the ulnare (distal to ulna), and the intermedium between them. The distal row contains five bones, the carpalia, numbered from one to five, beginning at the radial side. Between these two definite rows are several (often two or four) centralia. The bones of the ankle are similar, including a proximal row of three (tibiale, intermedium, and fibulare), a distal row of five (tarsalia), and an intermediate group of one to four bones (centralia).

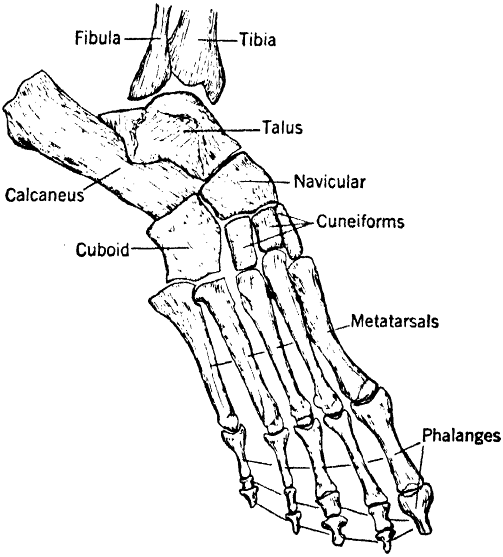


Fig. 233. The bones of the human foot.

Variations from this typical arrangement may result from the union of adjoining bones. In mammalian anatomy the bones of this region have long been known by different names (Figs. 231, 233).

The metacarpals and metatarsals are typically five in number (Fig. 229). These are referred to by number beginning with the pollex (thumb) and the hallux (great toe). There are also typically five rows of phalanges in each limb, the number of units in each row being subject to much variation in different forms. The number typical of mammals is 2, 3, 3, 3, 3; beginning with the first digit. All the bones of the appendages mentioned above are cartilage bones. Others, known as sesamoid bones, are present in this part of the skeleton in various vertebrates. These form by direct ossification in a tendon or some other connective tissue structure. The patella (kneecap) is an ossification in the tendon passing over the knee. The pisiform, which is characteristic of many mammals (Fig. 230), is a sesamoid bone on the ulnar side of the proximal row of carpals. Many other small sesamoid bones are often found on the under surface of either foot, at the joints between the phalanges.

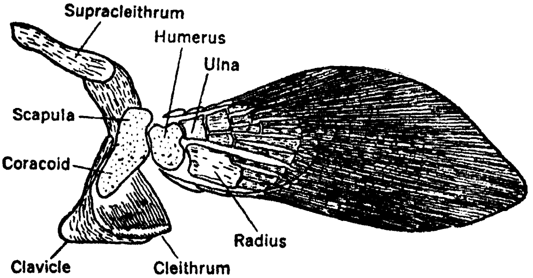


Fig. 234. Right pectoral fin of *Sauripterus taylori*, Upper Devonian. (From Lull, *Organic Evolution*, after W. K. Gregory, by permission of The Macmillan Company, publishers.)

PHYLOGENY OF THE APPENDICULAR SKELETON. It should be apparent from the above account that there is a striking homology between the appendages of all land-living vertebrates. Comparisons of parts in fishes and amphibia, however, are not so simple. A study of the embryology of the paired fins and of the tetrapod appendages, however, affords good evidence of their homologies. Both arise as longitudinal folds extending over several somites. Paleontology also furnishes corroborative evidence, most strikingly, perhaps, in *Sauripterus* (Fig. 234), a crossopterygian fish. In this interesting fossil, bones are present which are readily comparable to parts of the pectoral girdle, the humerus, radius, and ulna of existing tetrapod types (Fig. 235).

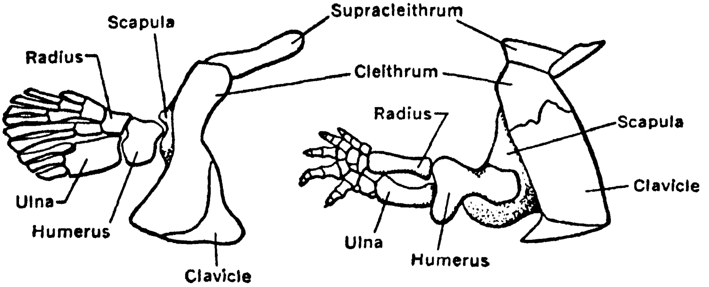


Fig. 235. The right pectoral limb (arm) and shoulder region of a lobe-finned fish (left) and a primitive amphibian (right), the latter turned back to a position comparable with the fish fin. (From Newman, *The Phylum Chordata*, after Romer, by permission of The Macmillan Company, publishers.)

The question of the origin of the paired fins has led to the formation of several theories. The most widely accepted theory (fin-fold) is based on a possible relation to the median fin system. According to this explanation, the median fin was

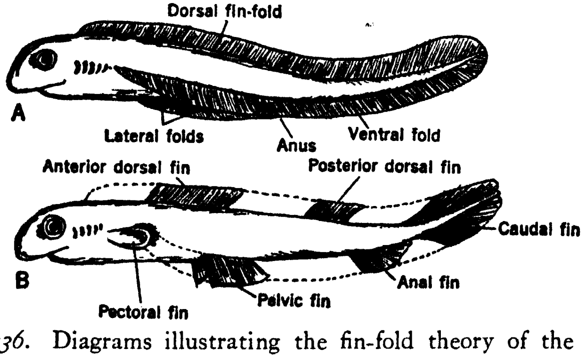


Fig. 236. Diagrams illustrating the fin-fold theory of the origin of median and paired fins of fishes. A, the undifferentiated condition with a continuous fin-fold; B, after parts of the continuous fold have been lost, leaving the fins characteristic of the typical fish. (Redrawn after Wiedersheim, by permission of The Macmillan Company, publishers.)

originally a continuous fold (Fig. 236), extending along the dorsal margin, around the tail, and ventrally as far forward as the cloacal opening. Here the fold bifurcated to pass around the opening and then continued forward as two lateral fin folds, almost to the head region. These folds were supported by a series of parallel rods, as are the median fins of the existing types. It has been suggested that in the course of time parts of this continuous fold have been lost, leaving one or more dorsal fins, a caudal and a ventral fin, as remaining portions of the median fold, and the pectorals and pelvics as portions of the paired lateral folds.

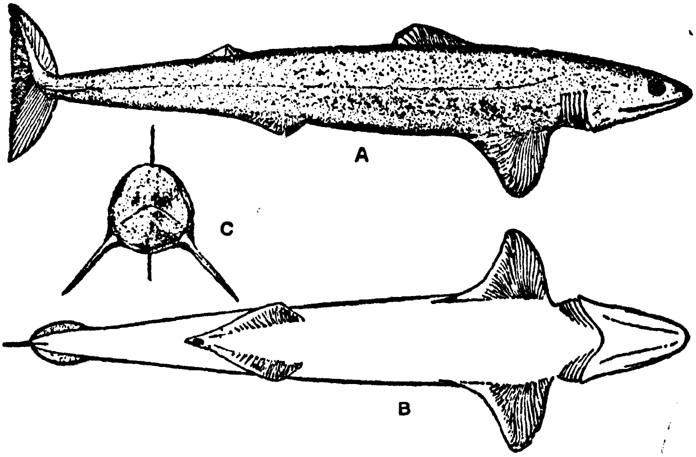


Fig. 237. Cladoselache fyleri, Upper Devonian, Ohio. A, right side view; B, ventral view; C, front view. Restored. (From Newman, *The Phylum Chordata*, after Woodward, by permission of The Macmillan Company, publishers.)

Amphioxus is usually cited as furnishing evidence tending to support this theory. The median fin is, of course, continuous, as in the theoretical condition, as far as the atriopore. It is not difficult to imagine that parts of the continuous fin have dropped out, leaving dorsal, caudal and ventral fins, which are so characteristic of fishes in general.

Homologies between the metapleural folds and the lateral folds required by the theory, however, seem rather doubtful. In *Amphioxus* bifurcation begins at the atriopore, an opening not retained by higher forms. Furthermore, no skeletal elements similar to those of the median fins are present in the metapleural folds.

The evidence furnished by *Cladoselache* (Fig. 237), an extinct selachian, seems more convincing. In this primitive shark, the paired fins are broad at the base, thus retaining the embryonic condition involving a number of somites. Moreover, the skeletal supports of these fins are slender, nearly parallel cartilages, as are those of the median fins.

An entirely satisfactory theory as to the origin of paired appendages awaits further and more convincing evidence.

SUMMARY

The vertebrate skeleton is an endoskeleton derived from mesoderm. The skeletal tissues are connective tissue, cartilage and bone. The former is derived from mesenchyme and may in time ossify, forming bone. Another kind of bone (dermal) develops directly from connective tissue in the dermis.

The skeleton is divided into three parts — axial, visceral, and appendicular. The axial skeleton includes the skull, the vertebrae, the ribs, and the sternum; the visceral consists of the upper and lower jaw, the hyoid arch and the branchial arches; and the appendicular includes the girdles (pectoral and pelvic) and the parts of the free (movable) limbs.

The beginnings of vertebrae are seen in the cyclostomes in the form of small cartilaginous processes at the sides of the nerve cord. In the elasmobranchs these processes have met dorsal to the nerve cord to form a complete neural arch which is still composed of cartilage. In the caudal region a similar arch, the haemal, develops ventral to the notochord, surrounding the caudal blood vessels. In other fishes the cartilage becomes more and more replaced by bone so that the vertebra of the typical teleost fish is a bony structure.

A typical vertebra consists of a body or centrum, a neural arch surrounding the nerve cord, a neural spine (dorsal to the arch) and transverse (lateral) processes. Articular processes (zygapophyses) bear surfaces for the articulation of adjoining vertebrae. There is differentiation of vertebrae in different regions of the body, particularly in the mammals in which are found cervical, thoracic, lumbar, sacral, and caudal vertebrae. The number of vertebrae in each region (with the exception of the caudal) is quite constant for a given species.

There are two kinds of ribs in vertebrates, the dorsal and the ventral. The dorsal ribs develop within the horizontal septa between the epaxial and hypaxial muscles. The ventral ribs originate just outside the peritoneal lining of the body cavity. The bird rib contains an uncinate process.

The sternum is a single bone or a series of bones in the median ventral region of the thorax. In the lower vertebrates it is more or less cartilaginous. In the higher ones it consists almost entirely of bone. The sternum of the flying birds is provided with a keel or carina, for the attachment of the powerful pectoral muscles.

The vertebrate skull appears first as a series of paired cartilages; the trabeculae in front of the notochord; the parachordals at the sides of the notochord; olfactory capsules around the olfactory organs; optic capsules around the eye and auditory (otic) capsules surrounding the ear. These increase in size until they unite (optic capsules excepted), the lateral margins grow dorsally and then medially to form a boxlike cartilage surrounding the brain. This phylogenetic stage in the development of the skull is represented in the skull of the adult elasmobranch. In other fishes bones of two kinds are present: membrane bones which develop in the skin and cartilage bones which form from centers of ossification within the cartilage. These two kinds of bones become more and more closely united in the higher vertebrates.

The typical amphibian skull is broad and flat and has two occipital condyles. A relatively large amount of cartilage is retained in the adult skull. The reptile skull is more bony and has a single median occipital condyle. In many reptiles there are large openings or fossae in the temporal region. The turtle skull is completely roofed over. The bird skull resembles that of the reptiles in the number of bones present and in having a single occipital condyle. It is composed of very thin and light bones which have united with one another giving greater strength. The mammal skull is relatively wide and deep and contains fewer bones, some having been lost while others have united to form bone complexes. Two occipital condyles are present.

The visceral skeleton consists of a series of arches surrounding the anterior part of the digestive tract. In the elasmobranchs these arches are made up of paired and median cartilages. The anterior arch (mandibular) consists of palatoquadrate (upper jaw) and Meckel's (lower jaw) cartilages. In other vertebrates membrane and cartilage bones develop around and in these paired cartilages to form the characteristic bony jaws. In birds and forms below them the articulation of the lower jaw is between the articular and the quadrate (cartilage bones). In the mammals a new articulation is present between dentary (lower jaw) and squamosal (upper jaw). The articular and quadrate have become respectively the malleus and incus located in the middle ear. The dentary is the only bone remaining in the lower jaw.

The second or hyoid arch of the elasmobranchs consists of paired cartilages, the dorsal hyomandibulars and the lateral ceratohyals and a median ventral basihyal. In bony fishes a series of membrane bones, the operculars, develop along the posterior edge of the arch. In higher forms a part of the hyomandibular ossifies, forming the columella (amphibians) or stapes (other classes) of the middle ear. Ossification of other parts of the arch gives rise to the series of hyoid bones which support the tongue. The branchial arches consist of various cartilages which support the gills in aquatic vertebrates. Portions of these remain in the mammals as the cartilages of the larynx and trachea.

The appendicular skeleton consists of the cartilages or bones of the appendages and of their supporting girdles. Two types of appendages are present in fishes, median and paired. The median fins are supported by bony or cartilaginous rods, the pterygiophores.

There are never more than two pairs of paired appendages in vertebrates, the anterior or pectoral and the posterior or pelvic. These are attached to the body by the pectoral and pelvic girdles. In elasmobranch fishes the girdles consist of cartilage. In other vertebrates various membrane and cartilage bones develop in relation to them. The most constant of these are the coracoid, clavicle, and scapula in the pectoral girdle; and the ilium, ischium, and pubis in the pelvic girdle. The pectoral girdle in most mammals consists largely of the scapula, the coracoid having united with it developmentally, forming the coracoid process. The clavicle, a dermal bone, is not present in all mammals. Articulating with the scapula at the glenoid fossa is a long bone, the humerus. Distal to this are two bones, the ulna and the radius. Next to these are a series of carpals. These are followed (distally) by a row of several metacarpals which are in turn followed by several rows of phalanges. In the hind limb a long bone, the femur, articulates with the girdle at the acetabulum. Articulating with this are two bones, the tibia and fibula. Next to these is a series of tarsals, which is followed in order by metatarsals and phalanges.

VIII. The Muscles

FUNCTION OF MUSCLES

Muscle tissue consists of cells in which the property of contractility is especially well developed. By the contraction of muscle tissue, motion of parts of the body in relation to other parts, and locomotion of an organism in relation to its environment, is produced. It is important to remember that any movement is caused by the contraction or shortening of the muscle fibers, and never by the lengthening or relaxation of them. Such a movement as the bending of the arm at the elbow (flexion) is caused by the contraction of muscles on the inner surface of the upper arm, while the opposite movement, the straightening of the arm (extension), is produced by the contraction of muscles on the outer surface of the same region. Muscles which produce opposite movements in this manner are said to be antagonistic in their action (Fig. 238).

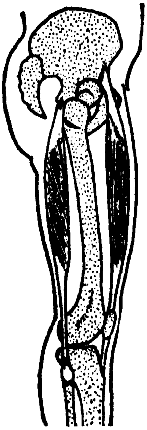


Fig. 238. Antagonistic muscles of the human leg. (From Walter, *Biology of the Vertebrates*, after Mollier, by permission of The Macmillan Company, publishers.)

KINDS OF MUSCLE TISSUE

On the basis of histological structure, muscle tissue may be classified into three kinds, smooth (Fig. 239), striated (Fig. 240), and cardiac. Smooth muscle cells are usually elongated and spindle shaped, with a typical nucleus in each cell. Striated muscle tissue differs from the preceding in that it consists of elongated fibrillae, or sarcostyles, which are marked transversely by alternate light and dark bands.

These bands cause the striated appearance which is characteristic of this type of muscle tissue. An indefinite number of nuclei will be seen among the striations. A tissue of this type, known as a syncytium, results from a series of cell divisions in which each division of the nucleus has not been followed by a division of the cytoplasm. The third type, or cardiac muscle, as found in the vertebrate heart, resembles the striated muscle in structure.

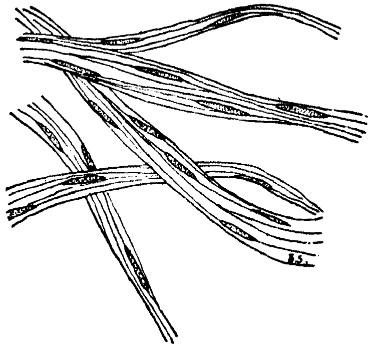


Fig. 239. Smooth muscle cells.

Physiologically, muscle tissue is said to be either voluntary or involuntary. Generally speaking, striated muscle tissue is voluntary (under the control of the will), while smooth muscle is involuntary. Exceptions may be noted in the case of cardiac muscles and certain muscles in the wall of the pharynx, esophagus, and bladder, which are striated in their structure but involuntary in their action.

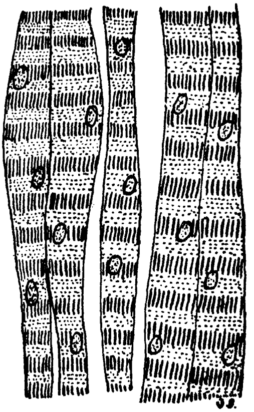


Fig. 240. Striated muscle tissue.

Smooth muscle cells are found in the walls of various organs of the body in association with other kinds of tissue. They are capable only of relatively slow and limited contraction, bringing about such motion as the rhythmic contraction of the intestine and other parts of the digestive system.

Cardiac muscle is derived from the modified walls of an enlarged blood vessel. Its origin, therefore, like that of smooth muscle, is from mesenchyme. Since both of these involuntary types are associated with various other tissues in the formation of organs, rather than being organs in themselves, it is natural to consider them in connection with a discussion of the various systems of the body.

Striated muscle, on the other hand, forms definite organs, structurally as well as functionally. The subsequent pages of this chapter will, therefore, deal only with the striated or voluntary muscles.

ORIGIN OF MUSCLES

As described above, muscles are of mesodermal origin, a great majority developing from the myotomes which originated in the dorsal portions of the mesoderm, the epimeres. A small number of muscles, those concerned with respiratory movements, are derived from the ventral portions of these segments, the hypomeres.

The main mass of muscles of the vertebrate body may be divided into three groups, axial, appendicular, and visceral, corresponding to the three divisions of the skeleton with which they are associated. Since the term visceral is naturally used when referring to the involuntary muscles of the various viscera, it is customary to use the word branchiomeric for those voluntary muscles associated with the visceral skeleton.

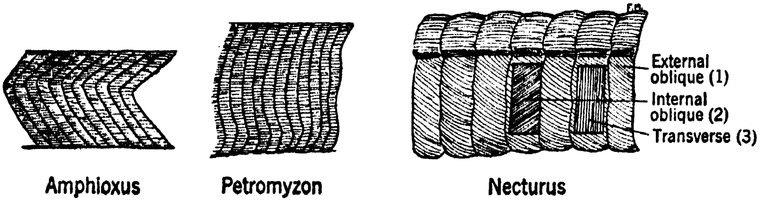


Fig. 241. Diagrams of muscles of the body wall.

The axial muscles are the oldest from the ontogenetic as well as the phylogenetic standpoint. As seen in their primitive condition, as in *Amphioxus*, the fishes, and *Necturus*, or in their embryonic condition, as in the embryo of higher vertebrates, the axial musculature consists of a series of segmentally arranged muscles, the myomeres (Fig. 241). These are separated from one another by transverse or diagonal sheets of connective tissue, the myosepta. The muscles of each side are further subdivided by a horizontal septum into two groups, a dorsal or epaxial, and a ventral or hypaxial, series. These muscles originally extend in an unbroken series from the base of the skull to the end of the tail. The development of paired appendages, either fins or limbs, with their accompanying appendicular muscles, has resulted in a profound modification of the axial musculature in these two regions of the body. In the adult of higher forms, the primitive arrangement is best seen in the muscles of the body wall and in those attached to the vertebrae and ribs.

The appendicular muscles are derived from the axial musculature of the corresponding region. In the development of the appendage a number of adjoining myomeres send out myotomic buds into the fold (Fig. 242). The myotomes just anterior and posterior to those immediately opposite the appendage often supply buds which take part in the formation of the appendicular muscles.

The branchiomeric muscles, as mentioned above, are derived from the hypomere. All three of these muscle groups, particularly the branchiomeric, may subsequently give rise to superficial muscles associated with the skin. These are known as integumentary muscles, and are often treated as a separate group.

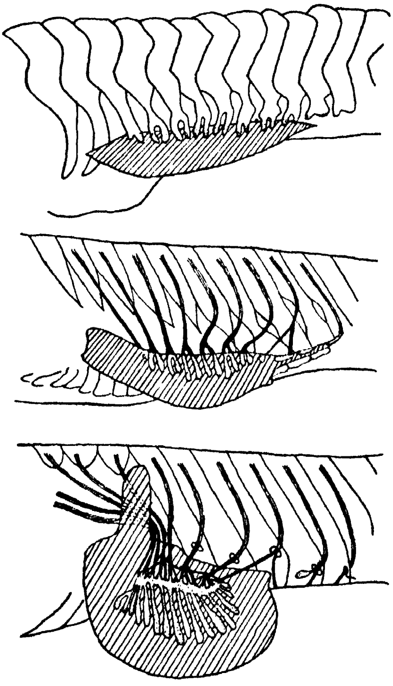


Fig. 242. Diagrams of the development of the pectoral fin in the dogfish. The muscle buds (stippled) with their corresponding nerves (black) are shown growing into the anlage of the fin (shaded). (Redrawn from Wilder, *The History of the Human Body*, after Braus, by permission of Henry Holt and Company.)

STRUCTURE OF A MUSCLE

The histology of muscle tissue has been described previously. The structural and functional unit which is known as a muscle consists of a number of striated muscle cells combined in a definite mass. A muscle is typically enclosed by a sheath of connective tissue, known as a fascia. A definite muscle may be separated into smaller bundles, or fasciculi, by connective tissue penetrating between groups of fibers.

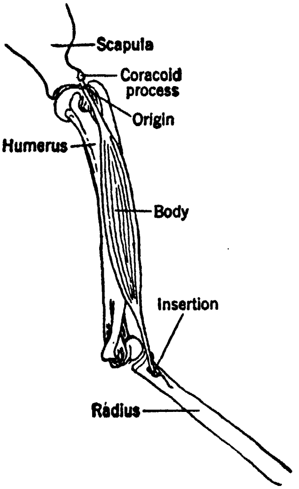


Fig. 243. Diagram of the biceps muscle of the cat showing its relation to the skeleton.

Most muscles of the vertebrates are attached to some part of the skeleton by means of their connective tissue sheaths which are continuous with similar sheaths (periosteal) surrounding the bones. This attachment may be spread out over a broad surface, as in the shoulder muscles, or confined within narrow limits, as in the distal attachments of appendicular muscles. When the connective tissue at the end of a muscle is drawn out to form a narrow cord or ribbon, it is known as a tendon. Both ends of a muscle may be attached directly to some part of the skeleton, or indirectly through the fascia covering some other muscle.

It was stated above that every muscular movement is brought about by the contraction or shortening of the fibers of which an individual muscle is composed. In producing any given movement, it is evident, therefore, that one end of the muscle involved is attached to a movable part of the skeleton, the other to a relatively immovable part. The end of a muscle attached to the structure which moves upon its contraction is called the insertion (Fig. 243); the opposite or more fixed end, its origin.

TYPES OF MOVEMENT

Voluntary muscles may be further classified according to the kinds of movement which they bring about. Among the more important kinds are the following:

Flexors — those producing a bending at a joint, as at the elbow or wrist
Extensors — those producing the opposite movement, as the straightening of a limb
Abductors — those moving an appendage or a part of the body away from the median line of the body
Adductors — those producing the opposite movement; namely, toward the median line
Elevators — those muscles which raise a structure in relation to others, as in the closing of the mouth by raising the lower jaw
Depressors — those producing the opposite movement, as the opening of the mouth by lowering the lower jaw
Rotators — those producing a rotary movement, as in the turning of the arm at the shoulder joint. Outward and inward rotators may be distinguished
Constrictors — muscles which close an opening, such as the sphincter muscles which close the eyelids
Dilators — those which enlarge a circular opening.

MUSCLE HOMOLOGIES

For several reasons it is very difficult to deal adequately with the phylogeny of the vertebrate muscles in a general discussion of this character. In the first place, the homologies of many muscles have not yet been satisfactorily determined; and secondly, because of this fact, several systems of nomenclature used for different groups have come to be well established in the literature.

The muscles of the human body were studied and named without following any consistent plan. The names of many human muscles are based upon such factors as shape (deltoideus) and location (supraspinatus) in relation to some particular part of the skeleton. In only a few cases (sternocleidomastoid) origins and insertions appear in the nomenclature. In still others the action of a muscle (levator scapulae) is included in its name. When comparative studies of the muscles of lower animals, such as the cat, were first made, new names were often applied. In more recent times investigators have come to give more consideration to the question of muscle homology, and have seen the desirability of using the same name for the muscles of different animals that are known to be homologous. An earnest attempt is being made to adopt a uniform terminology that will satisfactorily express the homologies that exist between the muscles of the different vertebrates. In the determination of muscle homologies, a number of factors may be considered. The natural tendency to consider as homologous those muscles which have a similar shape, location, and function is not satisfactory when applied in the case of two forms that are not closely related. Similarity of origin and insertion, while a somewhat more satisfactory basis, is not always reliable. In the case of appendicular muscles, where there is less possibility of variation in attachment, such features may well be considered sufficient. The reduction of certain bones and the loss of others would obviously cause changes in the origin or insertion of muscles originally attached to them. There are also many missing links encountered when one attempts to trace the phylogeny of muscles. The study of the marks of attachment of muscles upon the bones of fossils is contributing much interesting information to research workers in the field. The surest proof of muscle homologies is furnished by a study of their embryology, together with their innervation. It has been demonstrated that the nerve which supplies a given myotome continues to supply through its branches the various muscles which develop from the original element. The nerve supply is probably an absolute proof of muscle homology but it is very difficult to trace a given nerve fiber from its origin to the muscle which it innervates.

COMPARATIVE ANATOMY OF MUSCLES

AXIAL MUSCLES. It was stated above that the axial musculature is the oldest ontogenetically as well as phylogenetically. As seen in *Amphioxus*, the musculature, which may be considered entirely axial, consists of a series of V-shaped myomeres, separated from one another by myosepta. There is no differentiation in the myomeres except in their size, from the anterior to the posterior end. In the cyclostomes also, the myomeres are practically alike throughout the length of the animal. In *Amphioxus* and in the cyclostomes there is no horizontal septum.

In the fishes and all forms above them, following the greater development of the head, it is possible to divide the axial muscles into two groups, those of the head and those of the trunk (Fig. 244).

Head muscles. The most constant of the head muscles, those which move the eyeball, are derived from the three anterior myotomes. These muscles are clearly defined in the elasmobranchs and are subject to very little modification throughout the vertebrate classes. There are six muscles of the eyeball, the superior and inferior oblique, and the superior, inferior, external, and internal rectus. These are innervated by Nerves III, IV, and VI (Fig. 244) or by their branches. In all vertebrates above the amphibians, among other muscles in the head are those innervated by the Hypoglossal (Nerve XII). These are the muscles of the tongue, namely, hyoglossus, styloglossus, and genioglossus (Fig. 245), with the addition in the mammals of the lingualis.

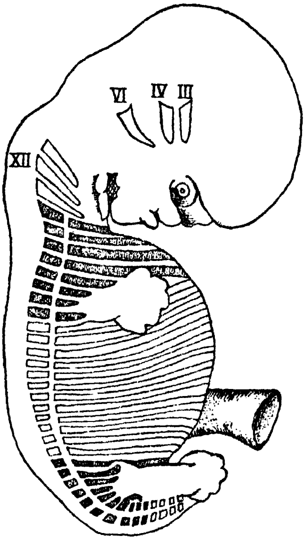


Fig. 244. Diagram of the metameric muscles of the human embryo. (Redrawn from Wilder, *The History of the Human Body*, after Piersol, by permission of Henry Holt and Company.)

Trunk muscles. In the cyclostomes, the muscles of the trunk and tail are undifferentiated, but in the fishes the horizontal septum divides the muscles of this region into dorsal and ventral portions. Those dorsal to the lateral line are referred to as epaxial muscles; those ventral to it, as the hypaxial. In all other respects the trunk muscles of the fishes retain their primitive characteristics, appearing as a series of myomeres separated by myosepta, much resembling the condition in *Amphioxus*, except that there are usually two V's, one above and one below the lateral line (Fig. 246).

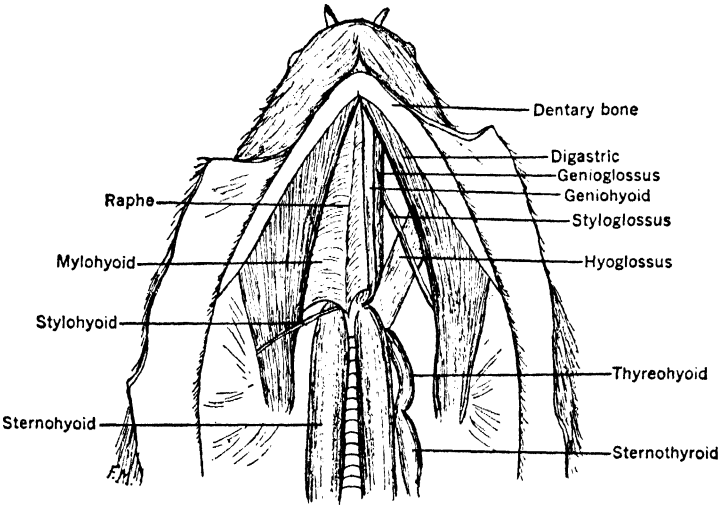


Fig. 245. Diagram of the muscles of the neck and tongue of the cat.

In the forms above the fishes, the differentiation of the epaxial musculature of the trunk is influenced by the development of the vertebrae and their various processes (Fig. 247). One of the largest muscles in this region is the longissimus dorsi, which occupies the space lateral to the neural spines and dorsal to the transverse processes. Many other shorter muscles are found in this region, where they appear in rather confusing series extending from one transverse process to another, from one neural spine to the next, or from the neural spine of one vertebra to the transverse process of the preceding.

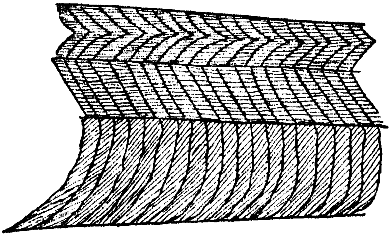


Fig. 246. Muscles of the body wall of the dogfish, *Squalus acanthias.*

In the birds, as a result of the more rigid union of the thoracic and lumbar vertebrae, these muscles are relatively unimportant, except in the neck region. In all vertebrates having paired appendages, the trunk musculature is greatly modified by the development of the appendicular muscles. This is more pronounced in the pelvic region than it is in the pectoral.

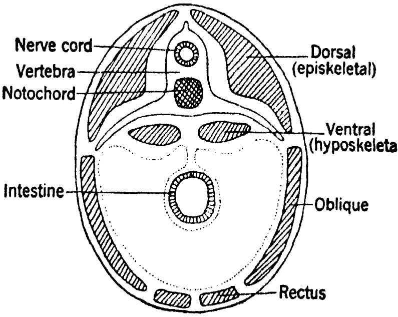


Fig. 247. Diagram of a cross section of a vertebrate showing the main groups of metameric muscles. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

The hypaxial muscles in classes above the fishes lose their primitive metameric arrangement, as the myosepta gradually disappear. Evidences of metamerism remain to some degree in the rectus abdominis, a thin, ribbonlike muscle developing along the mid-ventral line. In the posterior portion, this muscle, even in the mammals, retains its primitive character to some extent, since traces of the myosepta, known as tendinous inscriptions (Fig. 248), are still present crossing the longitudinal fibers. Anteriorly, this muscle is modified by the development of the sternum. As a result, it is broken up into a number of smaller muscles, such as the sternohyoid, sternothyroid, and thyrohyoid.

Laterally, the hypaxial muscles are typically divided into three thin layers, with the fibers running in different directions, in the different layers. These are in order passing from the skin inwardly, the external oblique, the internal oblique, and the transverse. The fibers of the two outer layers run diagonally and at right angles to each other, while those of the transverse run around the body, more nearly at right angles to its longitudinal axis.

With the development of the ribs, the oblique muscles in this region are broken up into external and internal intercostals, the fibers of which pass from one rib to the next.

Anterior to the ribs this group forms the scalenus muscles, and in the mammals it also gives rise to the serratus and the colli muscles of the neck.

The diaphragm, a dome-shaped muscular structure separating the thoracic and abdominal cavities in mammals, plays an important part in respiratory movements. It is derived from axial muscles in the ventral neck region, which shift their position backward.

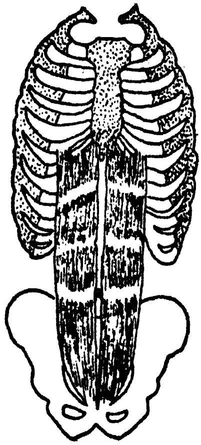


Fig. 248. The rectus abdominis muscles in man, showing the transverse tendinous inscriptions. (From Walter, *Biology of the Vertebrates*, after Mollier, by permission of The Macmillan Company, publishers.)

The myomeres of the tail region are important in the fishes because of the use of the caudal fin as an organ of locomotion. In those higher forms in which this structure is either lost or retained as a more or less ornamental device, the corresponding muscles are poorly developed.

Appendicular muscles. The appendicular muscles may be divided into two groups, extrinsic and intrinsic. In the former group are included those muscles by which the appendage is attached to the axial skeleton. Such muscles have their origin outside the appendage and their insertion upon some part of the skeleton within the limb. These muscles move the entire limb. Intrinsic muscles, on the other hand, have both origin and insertion within the limits of the appendage, and bring about movements of parts of the limb in relation to other parts.

The appendicular muscles of the fishes are not very clearly differentiated, and are not readily homologized with those of the higher classes in which the paired appendages have different functions. From the amphibians on, however, the phylogeny of many muscles in these groups may be traced with considerable assurance. In *Necturus*, for example, such extrinsic muscles as the trapezius, latissimus dorsi, pectoralis, levator scapulae, and serratus magnus are distinguishable in the fore limb. These same muscles, enlarged and modified, are present in the mammals (Fig. 249), while additional ones have been added, in many cases, as slips which have separated from them. The anterior edge of the latissimus dorsi, for example, separates from it to form the teres major. Similarly, the trapezius gives rise to the sterno- and cleidomastoideus.

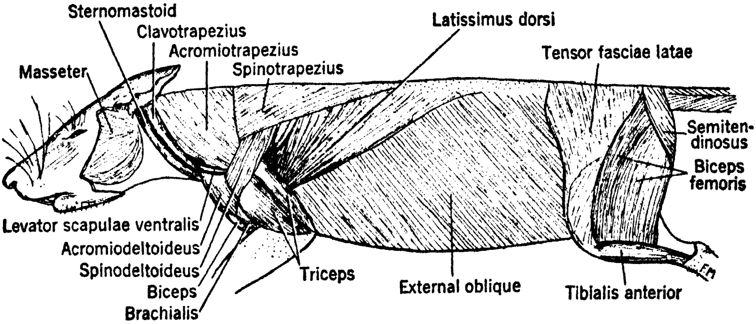


Fig. 249. The external muscles of the white rat.

Among the intrinsic muscles of the fore limb of *Necturus* may be mentioned the dorsalis scapulae, covering the scapula, the supracoracoideus on the coracoid, and the anconeus on the extensor side of the limb. It is considered probable that the first of these gives rise to the deltoid muscles of the mammals; the second, to the supraspinatus and the infraspinatus muscles; and the last named, to the various parts of the triceps.

In the pelvic limb also, similar muscle homologies may be traced from *Necturus* to the mammals, but much greater difficulty is encountered. The close attachment of the axial and appendicular skeletons in the pelvic region was referred to in the preceding chapter. This fusion of the pelvic girdle to the axial skeleton (sacrum) has brought about a more intimate relationship between the muscles of this region. This has made it more difficult to determine their homology.

BRANCHIOMERIC MUSCLES. It was stated above that the muscles associated with the splanchnocranium were derived from the hypomeres, the ventral portions of the mesodermal segments. These muscles appear in the fishes (Fig. 250) as an extensive series of levators, depressors, constrictors, dilators, etc., associated with the movements of a branchial respiratory device. The most anterior of these are related to the first visceral arch (mandibular) and give rise to such muscles as the temporalis and the masseter, used in raising the lower jaw, and, in higher forms, in mastication. The digastric muscle, which opens the mouth by depressing the lower jaw, is probably derived, in part at least, from portions of the muscles formerly attached to the second or hyoid arch. A few of the remaining muscles may be definitely traced in the higher vertebrates. Of the muscles of the second arch, the dorsal portion separates in the reptiles, forming the stapedius, which follows the stapes into the middle ear, while ventral portions give rise to the mylohyoid and the stylohyoid. The homologies of the remaining series of branchiomeric muscles have not been as definitely determined, although the possibility that they have followed the various cartilages entering into the formation of the larynx is strongly suggested.

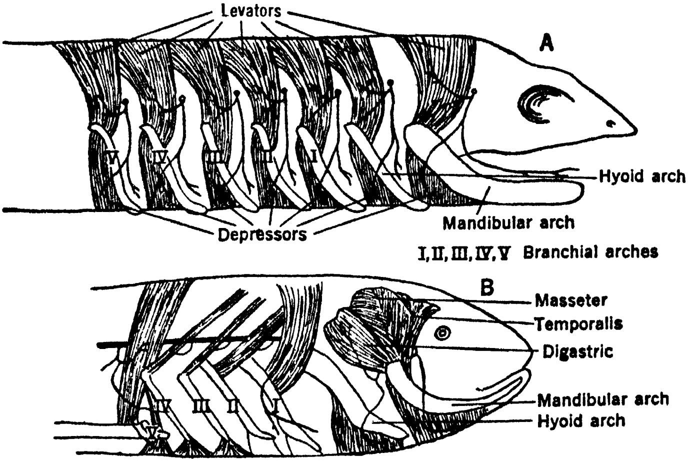


Fig. 250. Diagrams of branchiomeric muscles. A, a typical hypothetical form; B, arrangement in a typical urodele. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

Integumental muscles. This group of superficial muscles, derived by the splitting off of portions of the axial, appendicular, or branchiomeric musculature, is of little importance below the reptiles. In the snakes they play an important part in locomotion in the movements of the skin of the ventral surface of the body. In the birds the patagial muscles in the web of the wings, which assist in flight, are derived from the pectoralis muscles. In the mammals, the latissimus dorsi and the pectoralis give rise to an extensive sheet which may almost completely surround the thorax and abdomen. This is known as the panniculus carnosus (great cutaneus). Its action is well illustrated in the quivering of the skin of the horse (Fig. 251) in an attempt to dislodge a troublesome insect.

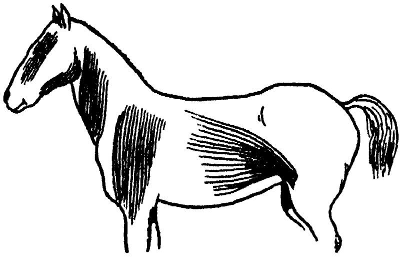


Fig. 251. The integumental muscles of a horse, by means of which the skin may be "shuddered" for dislodging annoying insects. These muscles are absent on the flanks, which can be reached by the swishing tail. (From Walter, *Biology of the Vertebrates*, after Nuhn, by permission of The Macmillan Company, publishers.)

In the cervical region of the reptiles, a similar sheet of muscle surrounds the neck with a thin layer of transverse fibers. This muscle, the sphincter colli, is a derivative of the branchiomeric muscles, as shown by its innervation. This is retained in much the same form by the birds, but in the mammals it is divided into two layers, the platysma and the sphincter colli. The former spreads out over the sides of the face, giving rise to numerous small muscles of the ear, eyebrow, nose, lips, and cheek. These facial muscles are particularly noticeable in man where they produce the variable expressions associated with human emotions.

SUMMARY

Muscles serve to bring about motion and locomotion. All muscular movement is brought about by the contraction or shortening of muscle fibers. Histologically there are three kinds of muscle tissue: smooth, striated, and cardiac. Striated muscle tissue is voluntary, while smooth and cardiac muscle is involuntary.

Voluntary muscles may be subdivided according to their relation to the skeleton into three groups: axial, appendicular, and visceral (branchiomeric). The axial muscles are originally segmentally arranged myomeres separated from one another by myosepta. In higher vertebrates this primitive condition is more and more obscured by the development of the appendicular muscles.

An individual muscle consists of a definite mass of muscle tissue surrounded by connective tissue (fascia). A muscle is typically attached at both ends to some part of the skeleton. The end attached to the movable part of the skeleton is known as the insertion, the other end as the origin. A given muscle has its own function to perform and, in terms of such functions, there are flexor, extensor, abductor, adductor, elevator, depressor, rotator, constrictor, and dilator muscles.

The best test of muscle homologies is furnished by a study of their embryology and their innervation. By such studies the homology of many of the more important muscles has been traced from the amphibians to the mammals. The six muscles of the eyeball are present in the elasmobranch fishes and in all vertebrates above them. Other constant muscles in the head region (above the amphibians) are the muscles of the tongue, innervated by the Hypoglossal (Nerve XII). The axial muscles of the trunk region are subject to much differentiation in the different vertebrates, depending upon the degree of development of the vertebrae.

Appendicular muscles are of two kinds, intrinsic and extrinsic. The former have both origin and insertion upon some part of the appendicular skeleton and bring about movements of parts of the appendage. Extrinsic muscles generally have their origin outside the appendage, and cause movement of the entire limb.

Branchiomeric muscles in fishes are concerned with the movements of the lower jaw and the gills. Of those associated with the mandibular arch, the temporalis, masseter, and digastric are constant throughout the vertebrates.

Integumental muscles are of importance in the reptiles, birds, and mammals.

IX. The Digestive System

The various processes of life in any organism result in the wearing out and breaking down of the cells of which the organism is composed. For development, for growth, and even for maintenance of life itself, new tissues must be formed to replace those worn out. This necessitates adding to the body from time to time those chemical elements of which the living substance, protoplasm, is composed. Since these chemicals outside the body occur in relatively complex combinations, it is necessary that they be simplified and made soluble before they can be utilized within the body in the formation or repair of living tissue. Digestion is that process which thus simplifies available food material. The digestive system includes those structures which are concerned with the intake of food, its mechanical and chemical preparation, and the elimination from the body of the remaining undigested waste material.

EMBRYOLOGY. The beginnings of the digestive system may be traced back to a very early stage in embryonic development. From the time of the formation of the two germ layers, the endoderm may be considered to be the forerunner of the digestive system since it remains as the epithelial lining of most of the adult digestive tract. The cavity of the gastrula, therefore, represents the beginning of the alimentary canal. As development continues, parts of the canal are differentiated (Fig. 252), forming the distinct organs which make up the functional digestive system of the adult. After giving rise to the notochord dorsally, the remaining endoderm (true or secondary endoderm) forms the epithelial lining of the canal and contributes largely to the formation of the liver, pancreas, and the respiratory organs. Associated with the endoderm in the formation of the various organs of the digestive system are such mesodermal tissues as peritoneum, connective tissue, blood vessels, and involuntary muscle.

As long as the embryo receives its food material from the yolk sac or through the maternal circulation (placental mammals), relations between the digestive tract and the outside world are unnecessary. When such a source of supply is no longer available and food must be obtained directly from the outside, a digestive tube with an inlet and an outlet is needed. In preparation for this time, ventral evaginations push out from the tube near the anterior and posterior ends. Just opposite these appear invaginations from the ectoderm. The anterior of these ectodermal pockets is the stomodaeum; the posterior one, the proctodaeum. These eventually meet the corresponding outpocketings of the tube, and the double layer of intervening cells breaks through, forming the mouth and anal openings. Because of this manner of development the digestive tract is lined for a short distance at either end with cells of ectodermal origin.

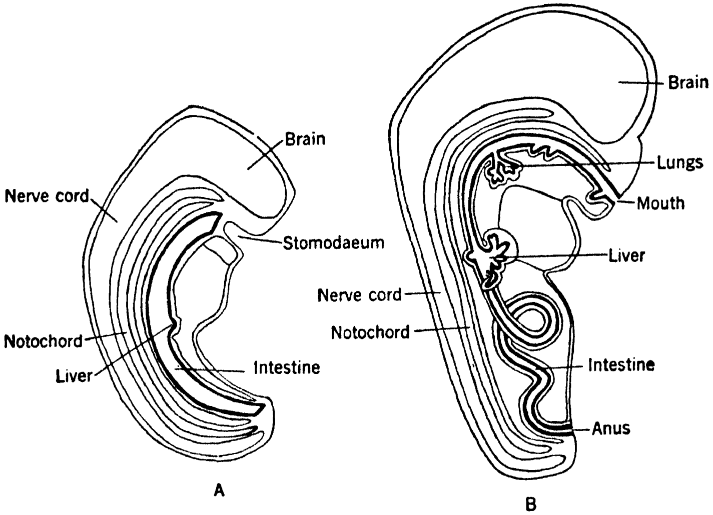


Fig. 252. Diagrams of longitudinal sections of vertebrate embryos showing development of parts of the digestive system. A, early stage; B, later stage. (Redrawn from Shull, *Principles of Animal Biology*, by permission of McGraw-Hill Book Company, Inc.)

As development continues from this simple condition, parts of the alimentary canal become modified, forming such differentiated parts as the pharynx, esophagus, stomach, intestine, and rectum; or, by evaginations at definite points, the canal gives rise to such structures as gills, lungs, swim bladders, caeca, and such digestive glands as the liver and pancreas. Each of these organs has a definite part to play in the digestive process.

HISTOLOGY OF THE ALIMENTARY CANAL. As seen in cross section (Fig. 253), the canal in the region of the small intestine consists of four layers surrounding the cavity, or lumen, of the tube. Beginning with the inner layer, these are, in order, the mucosa, submucosa, muscularis, and serosa. The mucosa is of endodermal origin, and from it are developed the various glands which produce the digestive juices. In this layer also are found smooth muscle cells, and blood and lymph vessels by which the prepared food is absorbed and distributed throughout the body. The submucosa is a thin protective layer of connective tissue. In the muscular coat are two layers of smooth muscle cells, an inner layer of circular muscles, and an outer layer of longitudinal muscles. The fourth and outer layer, the serosa, is a thin layer of peritoneum, continuous with the lining of the body cavity.

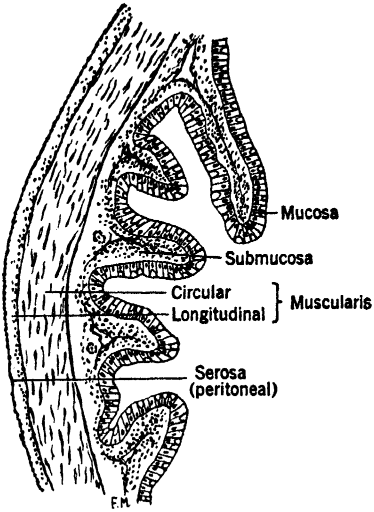


Fig. 253. Diagram of a small portion of a cross section of the frog's intestine showing its histology.

COMPARATIVE ANATOMY OF THE SYSTEM

In the following pages an account will be given of the different parts of the digestive system, as it is modified in the various vertebrate classes. The simple digestive tract of *Amphioxus* should be reviewed as a convenient starting point.

Cyclostomes. The digestive system of the members of this class is relatively simple. The mouth in some members is slightly ventral; in others, it is removed from the surface and is located within the cavity formed by the oral hood. It is a round opening which is opened and closed by the shortening or lengthening of a pistonlike tongue. Horny "teeth" are present in *Petromyzon* within the funnel and on the end of the tongue. These are wholly of epidermal origin and are not homologous to the teeth of other vertebrates. With the aid of these teeth, the tongue serves as a drill for boring into the bodies of other aquatic forms. The mouth opens into a cavity which divides posteriorly to form two tubes, the dorsal esophagus and the ventral respiratory tube. The esophagus is followed directly by the intestine, as there is no modification of that tract to form the stomach. The intestine is a slender, uncoiled tube terminating in the anus, which opens externally. A longitudinal fold, or ridge, within the intestine serves to increase slightly the area of the absorptive surface. This is known as the typhlosole; or, because of the fact that it winds spirally around the intestine, the spiral valve. A ventral outgrowth from the anterior end of the intestine is the liver. The tube connecting this structure with the intestine, known as the bile duct, is lost in the adult, so that the only communication with the digestive tract is through the blood stream. A rudimentary pancreas is present in the form of scattered patches of tissue in the wall of the intestine.

Fishes. In most elasmobranchs the mouth opens ventrally, instead of terminally as in the higher fishes. In this group and in all vertebrates above them, the mouth is opened or closed by the lowering or raising of the lower jaw. It was stated above that the outer margin of the mouth cavity is lined with ectoderm. In other words, the skin passes over the edge of the jaws into the mouth cavity. The placoid scales in this region of the skin are enlarged, forming teeth of the type characteristic of all vertebrates above the cyclostomes. As described in a previous chapter, the placoid scale consists of dentine which is of dermal origin. Although an epidermal enamel organ is present, as in the case of a developing tooth, it seems to contribute no material to the scale. The teeth of this class occur in several parallel rows, and are loosely attached to the skeleton of the jaw. When broken off or worn away they are replaced by new ones. Teeth which are replaced in this manner indefinitely are said to be polyphyodont. The elasmobranch teeth are all sharp and pointed with no variation in different parts of the tooth-bearing area. They are, therefore, said to be homodont.

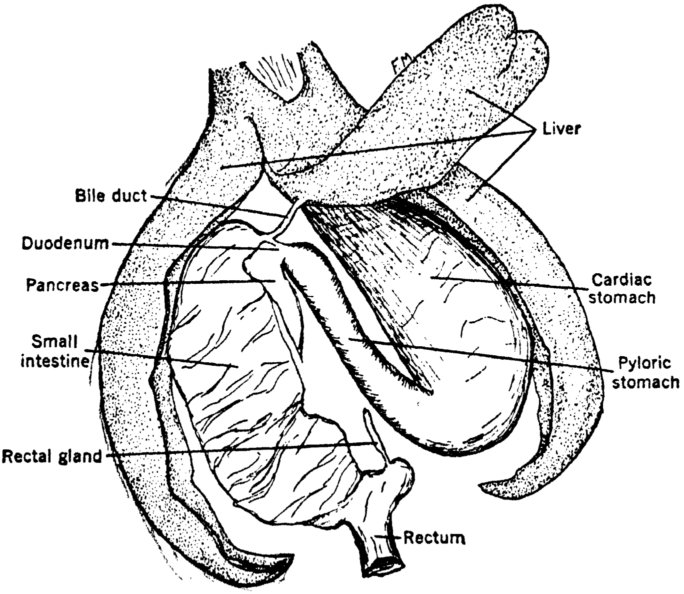


Fig. 254. The digestive system of the skate.

The mouth opens into the mouth cavity, which continues posteriorly as the pharynx. Opening into the lateral walls of the pharynx are the gill slits. These will be described in the following chapter on respiration. The esophagus, that portion of the alimentary canal between the pharynx and the stomach, is short and unmodified in all fishes. The stomach of elasmobranchs is typically J-shaped (Fig. 254), the large descending limb being the cardiac portion, the shorter ascending limb the pyloric region. At the posterior end is a constriction marking the location of the pyloric valve, a sphincter, between the stomach and the intestine. The intestine in this group may be divided into three definite regions, the duodenum, the "small" intestine, and the rectum. The duodenum is a short region just posterior to the pyloric valve. Two ducts usually enter this region, the bile duct from the liver, and the pancreatic duct from the pancreas. The "small" intestine is a widened portion of the tube following the duodenum. Although the largest part of the intestine in this group, it has the same function as the small intestine of higher forms. This narrows into the short rectum (large intestine), which terminates at the anal opening within the cloaca. This internal chamber, which also receives products of the reproductive and excretory systems, is characteristic of vertebrates, except in the case of higher fishes and the higher mammals. The rectal gland, an elongated, fingerlike diverticulum from the ventral floor of the rectum, is an organ of unknown function, characteristic of this group.

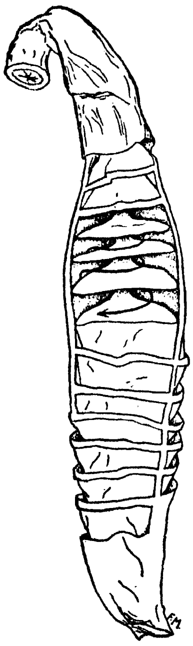


Fig. 255. Dissection of the spiral valve of the dogfish, *Squalus acanthias.*

The spiral valve (Fig. 255) of the dogfish is an important modification within the small intestine. Originating as a longitudinal fold, it becomes twisted spirally around the inner walls of the intestine. This structure not only provides greater surface for the absorption of food material by the blood stream, but also increases the time for digestion and absorption, by somewhat retarding the passage of food material through the canal.

In other fishes the digestive tract is essentially similar to that of the elasmobranchs, but shows various modifications of different regions. The mouth is typically terminal instead of ventral. A spiral valve is present in the Dipnoi, in some ganoids, and in at least one teleost. In all others, the absorptive surface is increased by means of pyloric caeca (Fig. 256). These are saclike diverticula developing from the tube just posterior to the pyloric stomach. In the teleost fishes the anus opens directly on the external surface instead of into a cloaca.

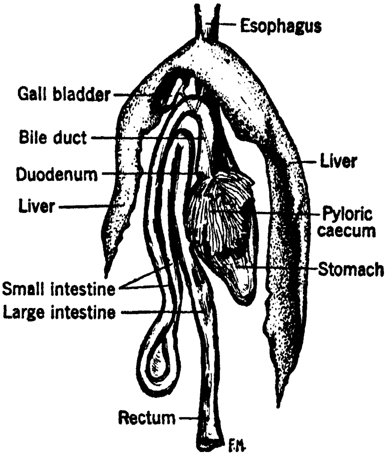


Fig. 256. The digestive system of the codfish.

Although a tongue appears for the first time in the fishes, it is not homologous to the structure of that name present in higher vertebrates. Consisting in this group of a membranous fold, supported by parts of the visceral skeleton, and moved indirectly by muscles attached to them, it does not play any considerable part in the mechanical preparation of food materials.

The teeth of the Osteichthyes and of all land vertebrates develop in a manner similar to that of the placoid scales, as has been described previously. Groups of cells of the Malpighian layer of the skin along the edge of the jaws, dip down into the underlying dermis (Fig. 257). They here form enamel organs which resemble inverted cups. The cavity of each cup is filled with cells of the dermis which form a dental papilla. The cells on the outer surface of the papilla, known as odontoblasts, secrete the dentine which makes up a greater

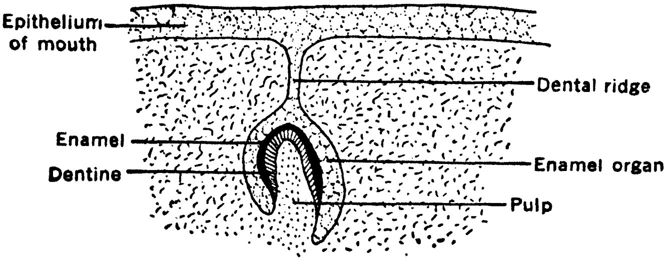


Fig. 257. Diagram to show origin of vertebrate tooth (lower jaw). (Reprinted by permission from *Introduction to Vertebrate Embryology*, Fourth Edition, by W. Shumway, published by John Wiley & Sons, Inc.)

part of the tooth. The cells on the inner surface of the enamel organ are known as ameloblasts. They secrete a crown of enamel over the outer portion of the dentine. The dental papilla remains as the pulp which contains nerve endings and capillaries which nourish the tooth. When the tooth is formed, its crown pushes upward and emerges above the surface of the membrane covering the jawbone. The roots of the tooth are surrounded by cement. This tissue, which aids in holding the tooth in place, is deposited by adjoining cells of the dermis.

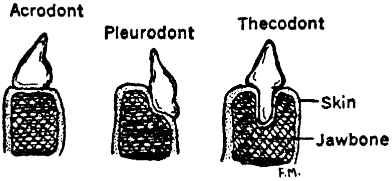


Fig. 258. Diagrams showing types of tooth attachment.

The teeth of fishes generally are homodont and polyphyodont, as was described above in the elasmobranchs. Although confined to the jaws in higher vertebrates, they are here found attached to numerous other parts of the skeleton, such as the vomer, palatine, and pterygoid bones, and the hyoid and branchial arches. The teeth of fishes are without roots, being attached loosely to the surface of the bony foundation. This type of attachment, the acrodont (Fig. 258), is characteristic of those forms having polyphyodont dentition.

The sturgeon, the seahorse, and the pipefish are among those fishes having no teeth.

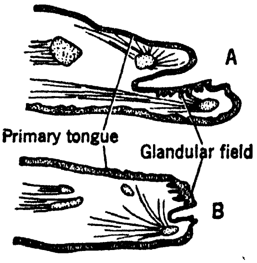


Fig. 259. Median sections through the floor of the mouth, showing the formation of the glandular tongue. A, *Triton alpestris;* B, *Salamandra maculosa.* In the latter the glandular field is encroaching upon the primary tongue to form the secondary tongue. (Redrawn from Walter, *Biology of the Vertebrates,* after Haller, by permission of The Macmillan Company, publishers.)

Amphibians. The digestive tract of the amphibian is also relatively simple. The mouth is terminal and in a majority of forms teeth are present. These teeth resemble those of the fishes in being homodont, polyphyodont, and acrodont. Teeth are lacking in the toads and in one of the urodeles (*Siren*), and in the frogs they are found only in the upper jaw.

In the lower amphibians, a primary tongue resembling that of the fishes is present. The so-called secondary tongue makes its appearance in the higher salamanders as an elevated glandular fold (Fig. 259), projecting anteriorly from the primary. This secondary tongue characteristic of higher vertebrates is invaded by intrinsic muscles which make possible a variety of movements. In the frogs and toads, the forked tongue is attached to the anterior part of the mouth cavity (Fig. 260), and when at rest its tip is withdrawn so that it points backward in the mouth cavity. In the capture of insects it may be rapidly shot out and then returned to its resting position, carrying its prey with it. Mucus, secreted by lingual glands of the tongue, aids in the capture of food.

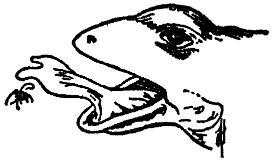


Fig. 260. Tongue of a frog, showing its attachment. (From Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

The pharynx, that portion of the canal between the mouth cavity and the esophagus, is not extensive. In the amphibians for the first time we find in this region a crossing of the two important incurrent pathways, that of the food and that of the air. This is known as the pharyngeal chiasma. In the preceding classes comprising water-living forms only, the respiratory medium, water, enters with the food and travels with it until making its exit through the gill slits. The nasal openings in a majority of these forms lead into blind sacs which do not communicate posteriorly with the pharynx. In the amphibians, however, with the development of the pulmonary (lung) system of respiration, the nasal cavities continue posteriorly and open directly into the mouth by the internal nares. A crossing of the air and food routes takes place, since the openings into the respiratory pathway, the external nares, are dorsal to the mouth, while the respiratory tube, the trachea, is ventral to the esophagus. In this class the internal nares are quite far forward in the mouth cavity.

The esophagus, especially in the frogs and toads, is very short and not clearly differentiated from the stomach. The latter organ in the amphibians is somewhat spindle-shaped, with the anterior end larger than the posterior. The stomach is separated from the intestine by the pyloric valve, containing a sphincter muscle.

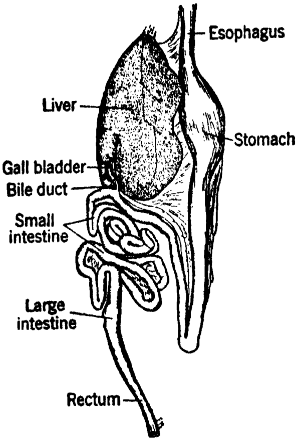


Fig. 261. The digestive system of *Cryptobranchus.*

With this class (Fig. 261) a greater distinction between the small and large intestine is apparent. The small intestine has increased in length, relative to that of the body, and therefore becomes slightly coiled. This results in increasing the area of the absorptive surface without the use of such modifications as spiral valves or pyloric caeca. The anterior portion of the small intestine, known as the duodenum, receives the secretion of the two important digestive glands, the liver and the pancreas. In the frog, the pancreatic ducts empty into the common bile duct which drains the liver. The remainder of the small intestine, the ileum, continues posteriorly to the enlarged part of the canal, the large intestine, or rectum, which opens into a cloaca.

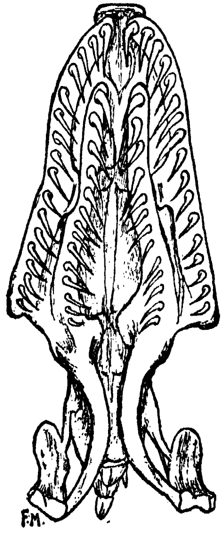


Fig. 262. Skull of python (ventral view), showing teeth attached to various bones.

Reptiles. The digestive tract in the reptiles is subject to much variation in the members of the different orders, but shows no great advance or modification over the preceding classes. The teeth are typically homodont, polyphyodont, and acrodont (Fig. 262). In some of the lizards, however, the teeth are attached to a shelf along the inner margin of the jaw bone, while in the alligators and crocodiles the teeth have roots which are set in sockets in the jaw. These types of attachment are known, respectively, as pleurodont and thecodont (Fig. 258). The members of the large order Testudinata are without teeth, the place of these structures (functionally) being taken by a horny beak of epidermal origin.

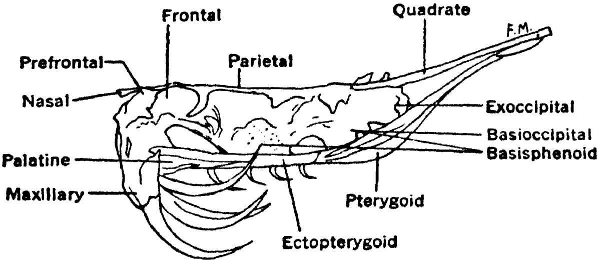


Fig. 263. Skull of rattlesnake, showing functional poison fangs and others ready to take their places.

The mouth glands in this class are much more definite in location and appearance. Palatine, lingual, sublingual, and labial glands may be distinguished. The poison glands of poisonous snakes are modified labial glands, while those of *Heloderma*, the poisonous lizard, are derived from the sublingual glands. The tongue of reptiles embryologically resembles that of the amphibians but it is attached posteriorly rather than anteriorly. In lizards and snakes it is often forked and highly protrusible. In the turtles and crocodiles, on the other hand, it is rather short and thick and much more limited in its movements.

The development of a secondary roof of the mouth, the hard palate, has carried the internal nares far back, so that the chiasma, or crossing of the respiratory and food routes, is now pharyngeal (Fig. 264).

The esophagus and stomach are not essentially different from these organs in the amphibians although a more definite division of the stomach into cardiac and pyloric regions is characteristic. In the crocodiles, the cardiac region is very much enlarged and, like the gizzard of birds, often contains stones.

The intestinal region (Fig. 265) is definitely divided into a small and large intestine. The small intestine of snakes is relatively straight, but, in other members of the class, is coiled. A new diverticulum, the colic caecum, develops at the junction between small and large intestine. This structure is small in the turtles but is well developed in other reptiles. The rectum opens into the cloaca through the anal opening.

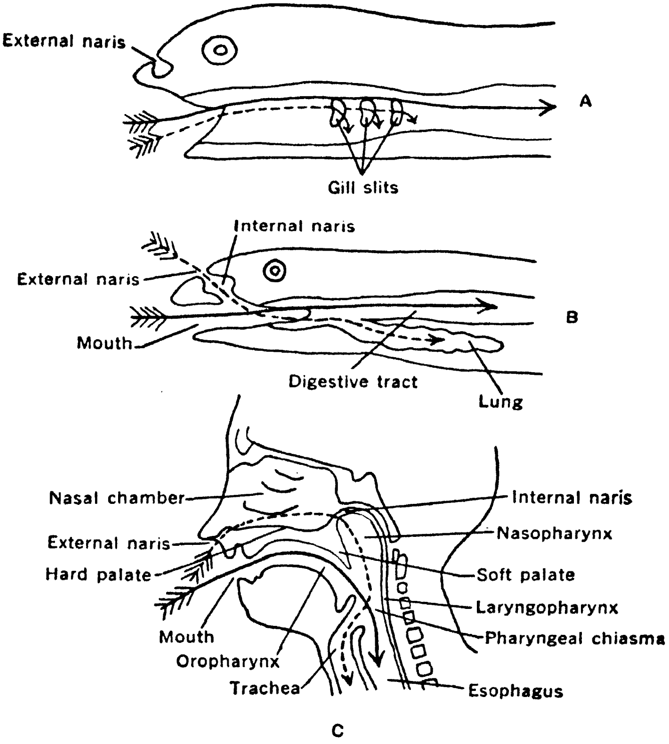


Fig. 264. Diagrams of the evolution of the pharyngeal chiasma. A, fish; B, reptile; C, man. The solid arrows indicate the course of the food, and the dotted arrows the course of the air. The position of the chiasma in man is pushed back as the result of the development of the hard palate. (Redrawn from Walter, *Biology of the Vertebrates*, after Wiedersheim, by permission of The Macmillan Company, publishers.)

Birds. The digestive tract of the birds is very similar to that of the reptiles, except for specializations of various parts. The presence of a horny beak and the absence of teeth are characteristics of all modern birds. The mouth is relatively dry because of the lack of mucous or salivary glands. The esophagus is long and has given rise to a lateral diverticulum known as the crop (Fig. 266). In some birds this is merely a temporary storage place; in others, the food within is chemically treated by secretions of glands in its walls. The stomach consists of two parts, the anterior glandular proventriculus and the posterior muscular-walled gizzard. In the gizzard mechanical breaking up of the food material is aided by the action of small pebbles and gravel. The gizzard is followed by the duodenum, which receives the pancreatic and bile ducts. The small intestine is much coiled, and there are typically two colic caeca at its junction with the short large intestine. The rectum opens into a cloaca through the anus.

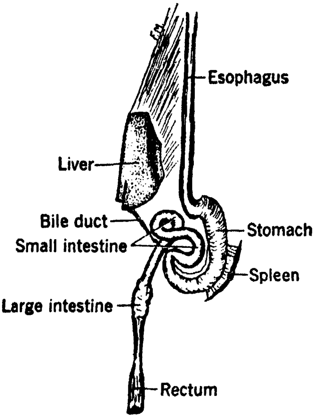


Fig. 265. The digestive system of a lizard, *Cnemidophorus.*

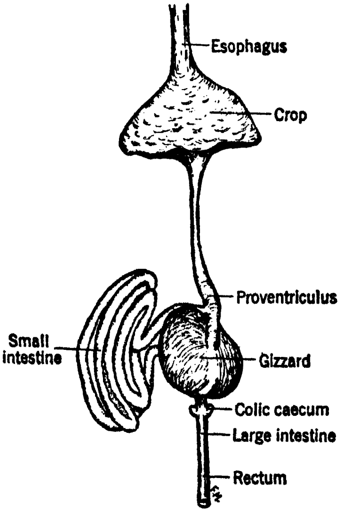


Fig. 266. The digestive system of the pigeon.

MAMMALS. The digestive tract of mammals is subject to much variation in the members of the different orders. Fleshy folds of the integument, the lips, surround the mouth, and laterally the loosely fitting skin forms distensible cheeks. Between the lips, the cheek, and the teeth is the buccal cavity (vestibule), a space practically obliterated when the lips are tightly closed. This cavity is widely distensible in squirrels and other rodents, forming the cheek pouches used as temporary storage places for nuts and other items of food.

Many mucous glands, the labial and molar glands, empty into this cavity. Stenson's duct, which opens just outside the upper molars, brings the secretion from the parotid, the largest of the salivary glands.

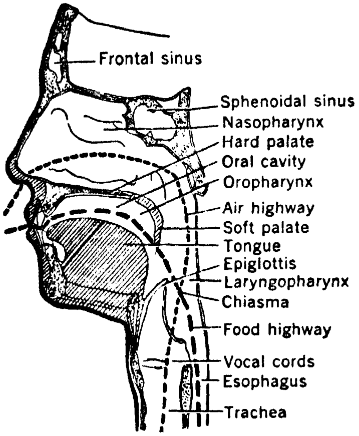


Fig. 267. Sagittal section through the head and throat of man, to show the pharyngeal chiasma. (From Walter, *Biology of the Vertebrates*, after Whitmarsh, by permission of The Macmillan Company, publishers.)

The teeth of mammals are subject to much variation in the different orders. Among the toothless mammals may be mentioned the monotremes, the scaly anteater, and many of the whales. With the exception of the toothed whales, the number is always definite and limited in contrast to the indefinite and unlimited number characteristic of other vertebrates. Mammals have but two sets of teeth during life, the first or milk dentition, followed by the second or permanent teeth. This condition is said to be diphyodont, as contrasted to the polyphyodont condition of other vertebrates. A tendency toward having a single set of teeth only (monophyodont) is apparent in some mammals. Marsupials retain all their milk teeth except the last premolars, while some of the moles never cut permanent teeth. Other mammals, such as bats and guinea pigs, are born with their permanent teeth in place, their milk teeth being shed "in utero."

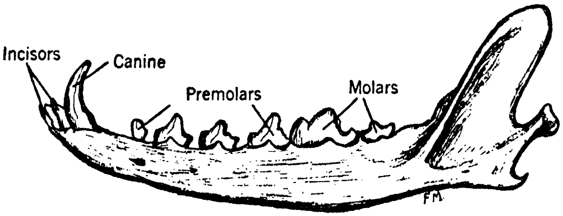


Fig. 268. The lower jaw of a mammal, the fox, showing heterodont dentition.

In the manner of attachment to the jaw bones, the mammalian teeth resemble those of crocodilians, having well-developed roots set in sockets (thecodont).

The teeth of mammals differ from those of all other living vertebrates in being subject to wide differentiation (Fig. 268) in different regions of the jaws. The anterior teeth, known as incisors, usually have sharp cutting edges. These are followed by the canines, which are typically round and pointed for the piercing and tearing of food. Posterior to these are the premolars and molars, which have a wide variety of surfaces provided with cusps and sharp overlapping edges for grinding and shearing purposes. The premolar teeth of an adult have been preceded by milk teeth, while the molar teeth have not. Mammalian teeth are said to be heterodont because of their differentiation. Among exceptions to this statement may be mentioned such mammals as the armadillo (Fig. 269) and the toothed whales, in which all the teeth are similar. In many herbivorous mammals, the canine teeth are missing, leaving a wide space between the incisors and premolars. Such a space between teeth is known as the diastema (Fig. 270). In some species certain teeth may become very much enlarged, forming tusks. These are usually formed from incisors or canines, and in many forms appear in the male only. The narwhal (*Monodon*) has a single tooth, an incisor, in the form of a long and spirally twisted tusk. In the elephant and walrus both sexes have tusks, in the former enlarged incisors and in the latter enlarged canines. In the incisors of rodents enamel is present on the anterior surface only. The anterior edge, therefore, wears away less rapidly,

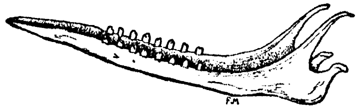


Fig. 269. Lower jaw of an edentate, *Dasypus* (an armadillo), showing homodont dentition.

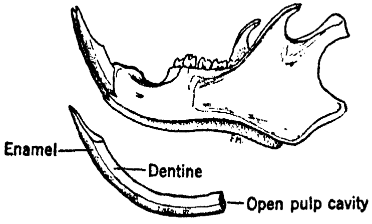


Fig. 270. The lower jaw of a woodchuck, *Marmota*, with an incisor tooth drawn to scale.

and as a result a permanent, chisel-like cutting edge is provided.

In most mammals the teeth grow to a certain size and then growth ceases as a result of the closing of the pulp cavity within (Fig. 271). Some, however, continue to grow throughout life, being provided with so-called "persistent pulps." Examples of these are tusks of the elephants and the incisors of rodents. In such teeth the pulp cavities remain open and the blood vessels within continue to supply food material to the odontoblasts. ✓

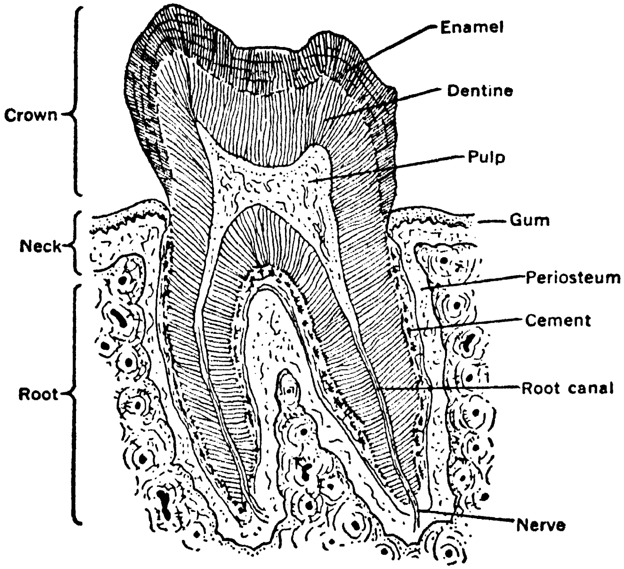


Fig. 271. Diagram of a human tooth, longitudinal section. (From Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

Each mammal has a definite number of teeth characteristic of the species, which may be expressed by the so-called dental formula. In man the dental formula is I 2/2, C 1/1, P 2/2, M 3/3. This means that there are two incisors on each half of the upper jaw with two on each half of the lower; one canine on each side of the upper jaw, and one on each side of the lower jaw; and so on for the premolars and molars. To obtain the total number of teeth present, it is necessary to add the number of different kinds of teeth on the upper and lower jaw and then multiply by two. The formula for the opossum is I 5/4, C 1/1, P 3/3, M 4/4; for the cat, I 3/3, C 1/1, P 3/2, M 1/1; and for the cow, I 0/3, C 0/0, P 3/3, M 3/3.

Several theories have been advanced to explain the origin of the complicated molar tooth of mammals. One of these, the concrescence theory suggested by Rose, assumes that the mammalian molar is the result of the fusion of separate cone-shaped teeth of the reptilian type. The more widely accepted theory, as advanced by Cope and Osborne, and elaborated upon by many others, may be called the differentiation theory. According to this theory the numerous cusps upon the crown of the tooth are buds, or outgrowths, of additional cusps upon the crown of a tooth that was originally conical. This theory is based upon considerable paleontological evidence. In early Triassic mammals the upper molars had three cusps, or cones, arranged in a longitudinal row. The longest cusp, the protocone, was in the middle with a smaller paracone in front and a metacone behind. The corresponding cusps in the lower molar were known as protoconid, paraconid, and metaconid. In addition to these three cones, a tooth of this type has a rim around the base of the crown known as the cingulum. Teeth of this type are said to be triconodont. A modification of this formation of cusps results in their arrangement in the form of a triangle. To bring about such a relationship, the two smaller cones of the upper jaw move inwards, those of the lower jaw outwards. The lower molars often develop a posterior depressed portion, the heel or talonid. Teeth of this type are referred to as tritubercular. Such an arrangement is characteristic of the molar of many fossil mammals. It has been handed down to a number of living forms, among which may be mentioned certain insectivores and the Virginia opossum, *Didelphis.*

The mouth, or oral cavity, is bounded anteriorly and laterally by the teeth. Its roof is formed by the hard palate anteriorly and the soft palate posteriorly. The hard palate is supported by the maxillary and palatine bones, and its surface often bears transverse folds, or ridges, the palatine rugae (Fig. 272). These are highly developed in cats, dogs, and other carnivores, and are evident in the human embryo. The soft palate is a flexible curtain of connective tissue, continuous with the hard palate and blending laterally with the walls of the mouth cavity. In man the median portion of the soft palate projects downward and backward as a rounded flap, the uvula. Numerous palatine glands secrete a mucus which aids in keeping the mouth cavity moist.

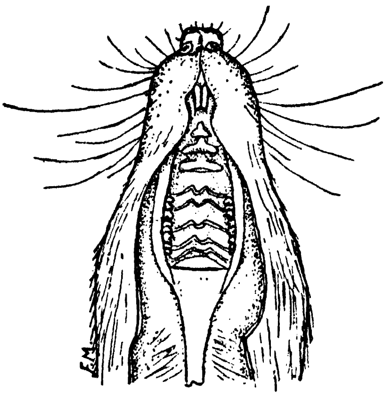


Fig. 272. Head of white rat with lower jaw removed and partially dissected to show hard palate and rugae.

The floor of the mouth cavity is largely formed by the tongue. This is highly muscular in mammals and capable of a variety of movements which aid in the manipulation of food in the mouth cavity. In herbivorous mammals it is highly prehensile. Taste buds, the organs concerned with the sense of taste, are numerous on the dorsal surface. Beneath the anterior margin of the tongue are openings of the ducts of the sublingual and submaxillary glands.

Posteriorly, the mouth cavity continues into the pharynx (Fig. 267). This may be divided into three regions: the oropharynx, ventral to the soft palate; the nasopharynx, dorsal to this structure; and, posteriorly, the laryngopharynx, all of which are intercommunicating. In the oropharynx are located the glandular lymphoid tissues commonly known as tonsils. The palatine tonsils are situated on the sides of the cavity, and the lingual tonsils on the posterior surface of the tongue.

The nasopharynx, which is concerned largely with respiration, will be discussed more fully in a later chapter. It contains similar lymphoid tissues — the pharyngeal tonsils, or adenoids. On either side are the openings of the eustachian tubes, leading from the cavity of the middle ear.

In the laryngopharynx is located the chiasma, the crossing of the digestive and respiratory pathways. Leading from this cavity posteriorly are two tubes, the digestive and respiratory tubes. The ventral of these is the trachea, or the respiratory tube. Its opening, or glottis, is protected by a triangular membrane, the epiglottis, which prevents the entrance of food. The dorsal or food tube is the esophagus. This is a muscular tube leading from the pharynx to the stomach. Its length varies with that of the neck, being approximately fourteen inches long in man.

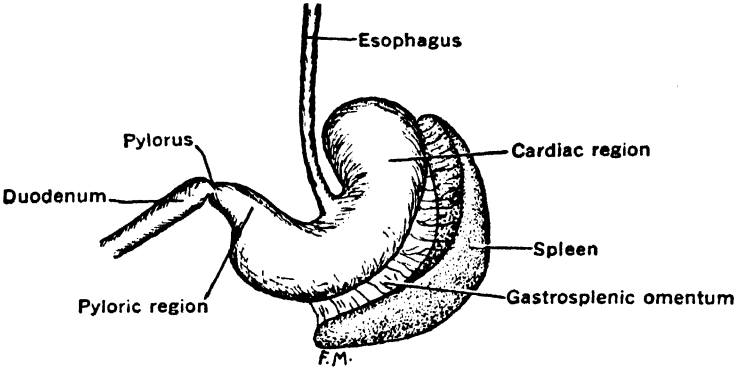


Fig. 273. Stomach of the white rat, showing its relation to the esophagus.

Various ductless glands located in relation to parts of the system are not directly concerned with digestion, and will be described in a subsequent chapter on endocrine glands.

The stomach of mammals (Fig. 273) is typically saclike in shape and usually lies transversely in the body cavity. In many forms it is possible to distinguish a cardiac from a pyloric region. The anterior, or concave, margin is known as the lesser curvature; the posterior, convex margin, as the greater curvature. The most highly specialized stomach is that of many ungulates (ruminants), which consists of four distinct chambers (Fig. 274). The first of these, the rumen, is a large storage space in which the food is temporarily held. From this chamber the contents pass unmodified into the second chamber, the reticulum, the walls of which are honeycombed. In these pits the grass is formed into compact "cuds" which are regurgitated into the mouth when the animal stops grazing. These "cuds" are then chewed over until sufficiently masticated, so that when swallowed the second time they pass by the opening into the rumen and enter directly the third chamber, the omasum. This leads in turn to the fourth and last chamber, the abomasum, the glandular part of the stomach, in which chemical modification is carried on.

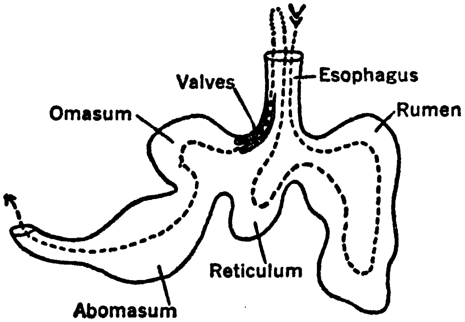


Fig. 274. Diagram of a ruminant stomach, with dotted lines showing the course of the food. (From Walter, *Biology of the Vertebrates*, after Hesse, by permission of The Macmillan Company, publishers.)

The small intestine of mammals is long and thrown into many coils. It may be divided into three more or less distinct regions, the duodenum, jejunum, and ileum. The anterior region, the duodenum, is separated from the stomach by the pyloric valve. It is a relatively short tube into which the bile and pancreatic ducts empty. The jejunum, or middle portion, is longer than the duodenum; the walls are thicker and more richly supplied with blood vessels. The posterior ileum includes the greater part of the small intestine. The inner surface of the small intestine in this class is greatly increased by numerous fingerlike projections, or villi, which extend from its walls into the lumen.

At the junction between the small and large intestine, a colic caecum (Fig. 275) is usually present. This structure is particularly large in herbivorous mammals, while it is small or missing in many carnivorous forms. In many mammals, as in some rodents, monkeys, and man, the blind end of the caecum is a degenerate structure, the vermiform appendix.

The large intestine includes the colon and rectum. In many mammals the colon may be divided into three regions, the ascending, transverse, and descending colon. In man and to a lesser degree in other mammals, the colon has a ruffled appearance due to the presence of three narrow bands of longitudinal muscles, the taeniae coli. These are quite short when compared to the length of the colon. As a result, three rows of small pouches, the haustra, extend along its entire length. In the monotremes the rectum opens into a cloaca, but in all other mammals the anus is a separate external opening closed by a voluntary sphincter muscle.

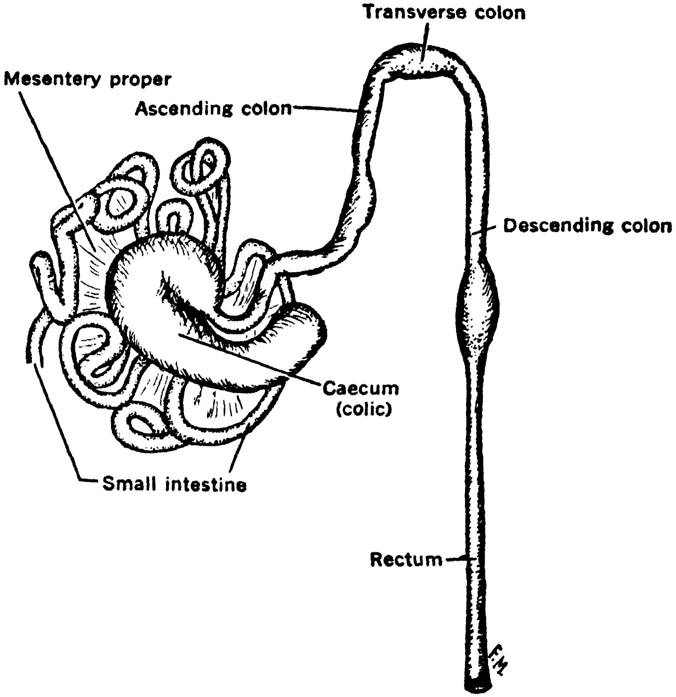


Fig. 275. The caecum of a white rat, ventral view, showing its relation to the intestine.

THE DIGESTIVE GLANDS

In the preceding description of the digestive system various glands associated with it have been mentioned. Among these glands which play an important part in the preparation of food are mucous, salivary, gastric, and intestinal glands, and the liver and pancreas. Mucous glands are not present in aquatic vertebrates nor in birds. Found in the mouth cavity and the large intestine, their secretion serves to moisten food preparatory to swallowing, or to provide lubrication for the passage of waste from the body. Of the salivary glands, which are especially well developed in mammals, the more constant are the parotid (Fig. 276), submaxillary, and sublingual. The parotid gland is usually the largest of these and is located just beneath the skin ventral to the ear. It communicates with the buccal cavity by means of Stenson's duct. The submaxillary gland is somewhat ventral to the parotid while the sublingual, as the name implies, is beneath the tongue. Wharton's duct from the submaxillary, and the ducts of Rivini from the sublingual gland empty into the oral cavity.

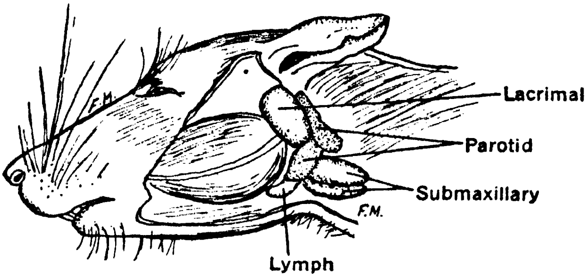


Fig. 276. Head and neck of the white rat, showing salivary and other glands.

The gastric glands, located in the lining of the stomach, secrete the gastric juice, while in the small intestine the glands of Brunner and of Lieberkühn secrete the intestinal juices. The gastric and intestinal juices both play an important part in the chemical modification of food.

The liver (Fig. 277) is the largest of the digestive glands and usually the largest organ of the body. It arises as a ventral diverticulum from the alimentary canal near the beginning of the small intestine. As this enlarges and grows forward, the anterior portion becomes the glandular part, while the posterior portion, near its place of origin, develops into the gall bladder and the ducts. The liver of *Amphioxus* is a single sac projecting anteriorly on the right side of the pharynx. In most vertebrates it consists of at least two lobes, a right and a left. In man five lobes are distinguished, and in dogs seven. The gall bladder is a thin-walled sac embedded in the liver and serving as a storage reservoir for the bile secreted by the liver cells. In many herbivores the gall bladder is missing. The numerous channels between the glandular cells of the liver lead to larger tubes, the hepatic ducts (Fig. 278), which unite to form the common bile duct, which empties into the duodenum. When a gall bladder is present it may be considered to be a diverticulum from the common bile duct, with which it retains its connection through the cystic duct.

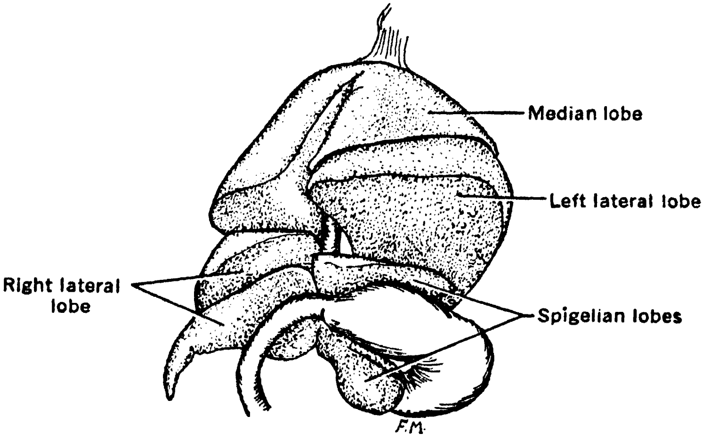


Fig. 277. Liver and stomach of the white rat, ventral view.

Although embryologically a part of the digestive system, the liver has a number of functions, besides that of secreting bile which plays an indirect part in the chemical preparation of food. The liver also takes part in excretion by the formation of urea; it serves as a temporary storage place for reserve food material in the form of glycogen; and it regulates the contents of the blood as this fluid passes through its tissue in the capillaries of the hepatic portal system.

The second largest gland associated with the digestive system is the pancreas (Fig. 278). This is a compound alveolar gland, diffuse in character, usually located in the curve between the stomach and the duodenum. It develops as one or more evaginations from the alimentary canal, somewhat posterior to that forming the liver. In some animals there are both dorsal and ventral diverticula, which may later unite. The duct of the dorsal portion is known as the duct of Santorini; that of the ventral lobes, as Wirsung's duct. In the lamprey the ducts are lost and the secretion is distributed by the blood. In some forms the various ducts unite, forming a single pancreatic duct which empties directly into the duodenum. In others the pancreatic duct joins the bile duct.

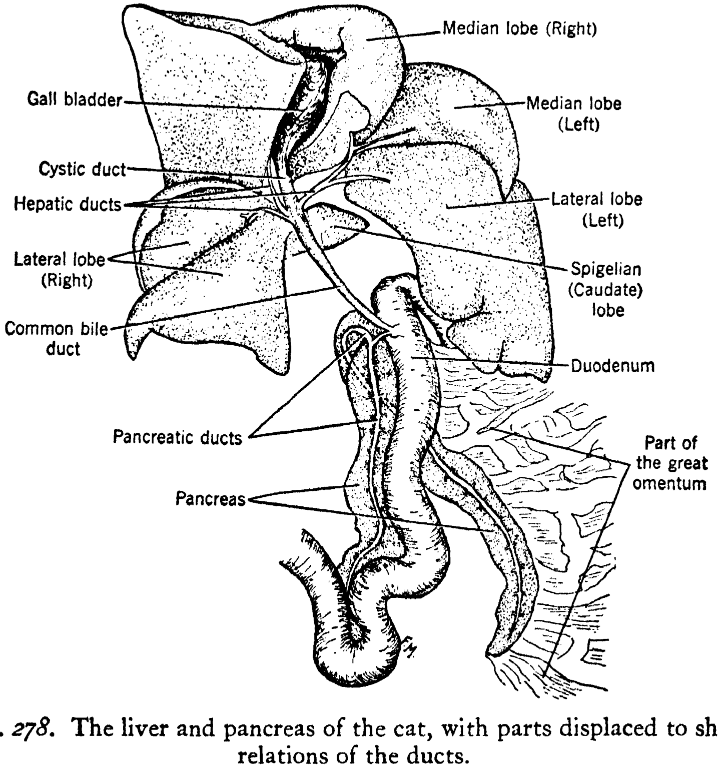


Fig. 278. The liver and pancreas of the cat, with parts displaced to show relations of the ducts.

Histologically, the pancreas consists of two different types of cells, those concerned with the secretion of pancreatic juice, and others arranged in irregular groups, the Islands of Langerhans, which secrete a material very different in character and function. The second type of cell constitutes a part of the system of ductless, or endocrine, glands, which will be discussed in a separate chapter.

FUNCTION OF THE DIGESTIVE ORGANS

It was previously stated that digestion is a combination of both chemical and physical processes. Now that the various structures making up the digestive system have been described, it will be of interest to consider briefly the functions of these different organs.

The mouth is concerned largely with the seizing of food and its subsequent mechanical preparation. In the lower vertebrates the teeth are used chiefly in seizing food, preventing its escape, and, with the aid of the tongue, forcing it along to other parts of the system. In toothless forms like birds and turtles, the beak has a similar function. The food is quite generally swallowed whole after being moistened by the secretions of mucous glands. In mammals, which have heterodont dentition, food is not only seized but cut, torn, ground, and mixed with saliva by the action of the teeth aided by the cheeks and tongue.

In vertebrates having salivary glands, chemical preparation is begun by the action of the enzymes amylase and maltase, which change starches to simple sugars.

The esophagus functions chiefly in a mechanical manner, the rhythmic contraction of its muscular walls forcing the food on toward the stomach. During this time the action of the enzymes of the salivary glands continues. In some birds, glands are present in the crop, and their secretion aids in the chemical modification of food.

The stomach has at least three functions, those of storage, mechanical mixing, and chemical modification. The presence of a temporary storage place has given the vertebrates a great advantage over lower forms of animal life, in making continuous feeding unnecessary. Mechanically, the food is thoroughly churned and mixed by the action of the muscular walls of the stomach. The function of the gizzard of the birds has been mentioned before. Glands in the stomach wall secrete gastric juice which contains hydrochloric acid, pepsin, rennin, and lipase. In the presence of acid, pepsin breaks down proteins to peptones. Casein, an insoluble material, produced by the coagulation of milk by the action of rennin, is changed to a soluble substance by pepsin. The breaking up of fats is begun by the lipase.

The final steps in the chemical preparation of food occur in the small intestine. Brunner's glands produce an alkaline secretion which makes possible the continuation of the activity of pepsin, begun in the stomach. Pancreatic juice is an alkaline secretion containing: amylopsin, which continues the process of changing starches to sugars; trypsin, which continues the modification of proteins, forming amino acids; and steapsin, which acts upon fats, changing them to fatty acids and glycerol. Bile, secreted by the liver, furnishes the alkaline medium in which the action of steapsin is hastened. The glands of Lieberkühn also secrete an alkaline juice containing enterokinase and erepsin, which complete protein digestion, and maltase, which furthers that of carbohydrates.

When all digestible parts of the food taken in are thus prepared, the resulting amino acids, sugars, soaps, and glycerol pass in solution through the walls of the intestine into the capillaries, by the process known as absorption.

The remaining undigestible material consisting of connective tissues, cellulose, and undigested fats, together with water and bile, pass on through the large intestine and rectum. Small amounts of water and bile are absorbed through its walls into the blood stream. The remainder of the undigested matter, lubricated by the secretion of mucous glands in this region, passes out of the system through the anus.

SUMMARY

The digestive system is that system concerned with the intake of food, its mechanical and chemical preparation, and the elimination of remaining waste materials. The beginning of the vertebrate digestive system may be traced back to the gastrula stage of the embryo, the primitive endoderm forming the lining of most of the digestive canal. As development continues, other tissues are added and the different regions of the canal are differentiated, giving rise to the various organs characteristic of the species.

The alimentary canal in cross section consists of four regions or layers of tissue, surrounding a central cavity. These are, in order, beginning with the outermost layer, the serosa (continuous with the peritoneum), muscularis, submucosa, and mucosa.

In the cyclostomes, the digestive system consists of pharynx, esophagus, liver, intestine, and anus. The intestine is straight and unmodified except for an internal fold which slightly increases its internal surface.

From the fishes on, teeth are present and play an important part in the mechanical modification of food. The system is relatively simple in this class. The pharynx is concerned also with respiration. The intestine is relatively straight and is modified by such structures as the spiral valve and rectal gland of the elasmobranchs and the pyloric caeca in the teleosts. The anterior portion or duodenum receives ducts from the liver and pancreas. A cloaca is present in the elasmobranchs but not in the teleosts. Liver and pancreas are well developed.

The amphibian digestive system also is relatively simple. In the pharynx a crossing of food and respiratory pathways takes place. The esophagus is relatively short. The intestine has increased in length and there is a more definite distinction between the small and large intestine. The former is slightly coiled and consists of duodenum and ileum. The large intestine opens into a cloaca.

In the reptiles the system is essentially similar to that of the amphibians. Various glands opening into the mouth are more definite. In some species certain of these are modified forming poison glands. The small intestine, except in the snakes, is coiled. A caecum (colic) is present in many at the junction between the small and large intestine. The rectum opens into a cloaca.

The absence of teeth is characteristic of modern birds. Mucous and salivary glands are also absent. The crop, a diverticulum from the esophagus, serves as a storage place. The stomach consists of an anterior (glandular) proventriculus, and a posterior (muscular) gizzard. Two colic caeca and a cloaca are present.

In the mammals the mouth is surrounded by fleshy lips and distensible cheeks. Mucous and salivary glands open into the mouth cavity. The teeth are differentiated (heterodont). The most complicated stomach is the four-chambered structure found in many of the ungulates. The small intestine is long and contains many coils. It consists of three regions, duodenum, jejunum, and ileum. A colic caecum is present. The large intestine often consists of an ascending, a transverse, and a descending colon. The latter leads into the rectum which continues to an external opening, the anus. A cloaca is present in the monotremes only.

X. *The Respiratory System*

FUNCTIONS

A living animal, although composed of the same chemical elements as nonliving things, differs from them in many ways, among which may be mentioned its ability to move. In the production of motion within the body and locomotion of the entire body in relation to others, energy is expended. The source of the necessary energy is the food materials prepared by the digestive system (as described in the preceding chapter) and then distributed by the blood stream throughout the body and assimilated or stored in the cells. To be utilized, this energy must be liberated by the combustion of the materials within the cells, and for any combustion process the presence of oxygen is required. As a result of the combination of oxygen and the elements within the tissue cells, energy is liberated in various forms, such as body heat, muscular movement, and the production of glandular secretions. As in similar chemical processes outside of the body of a living organism, waste products are formed and these must be removed if the process is to continue uninterrupted.

The respiratory system includes those organs which are concerned with the delivery of oxygen to the transportation system (blood stream) and with the elimination of the gaseous waste products of metabolism. In its broadest sense respiration also includes the passage of oxygen from the blood stream to the tissue cells and the subsequent changes taking place within them. This phase of the respiratory process may be called internal respiration, in contrast to external respiration, which includes the exchange between the external medium and the blood stream. Morphologically, it is customary to consider as the organs of respiration those concerned with external respiration only.

FUNDAMENTALS OF A RESPIRATORY MECHANISM

A respiratory organ, of whatever type, consists of a thin membrane, on one side of which is the respiratory medium, and on the other the distributing medium (Fig. 279). The respiratory medium is that medium containing oxygen, and is, therefore, either water or air. The circulating medium is the blood stream. To make possible an exchange of gases (oxygen and carbon dioxide) through this membrane, it must be kept moist. It then becomes a semipermeable membrane through which these gases may pass by osmosis.

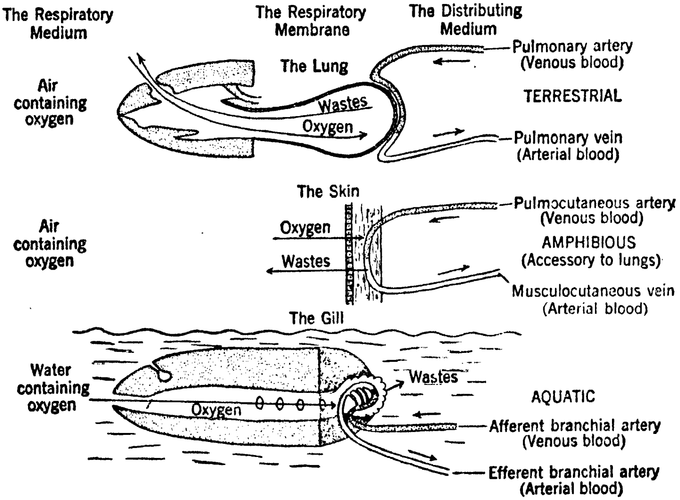

The Respiratory Medium
The Respiratory Membrane
The Distributing Medium
Air containing oxygen
The Lung
Wastes
Oxygen
Pulmonary artery (Venous blood)
TERRESTRIAL
Pulmonary vein (Arterial blood)
The Skin
Air containing oxygen
Oxygen
Wastes
Pulmocutaneous artery (Venous blood)
AMPHIBIOUS (Accessory to lungs)
Musculocutaneous vein (Arterial blood)
The Gill
Water containing oxygen
Oxygen
Wastes
AQUATIC
Afferent branchial artery (Venous blood)
Efferent branchial artery (Arterial blood)

Fig. 279. Diagrams illustrating the essential parts of the vertebrate respiratory system.

TYPES OF SYSTEMS

The chief organs of respiration in the vertebrates are gills and lungs. Although differing greatly in general appearance, both types are made up of thin membranes richly supplied with blood vessels. In aquatic forms generally, the respiratory organs are gills, bathed by water entering the mouth, and passing out through gill slits. In terrestrial vertebrates, lungs serve as the respiratory organs. Located within the body for protection from injury or desiccation, they are in communication with the respiratory medium, air, by means of tubes. In the amphibians in general, gills of a different type (external) are functional in the larval stages, but are replaced by lungs in the adult. In some amphibians, such as the permanently aquatic *Necturus*, gills are functional throughout life, although very simple lungs develop. The function of the skin as an accessory respiratory membrane in many amphibians should also be mentioned. Moistened by the secretion of mucous glands and richly supplied with blood vessels, the skin has the necessary features of a respiratory membrane. Indeed, in some amphibians, the skin appears to be a more efficient organ of respiration than the lungs.

Any respiratory system, whether of the branchial (gill) or pulmonary (lung) type, includes also various accessory structures which serve either to protect the membrane or keep it moist; or to provide for a continuous supply of the respiratory medium.

EMBRYOLOGY

We have previously seen that one of the most important characteristics of the chordates is the presence of a pharyngeal breathing mechanism at some time during its life history. In the development of the vertebrate respiratory system, one of the first steps noted is the formation of the pharyngeal pouches (Fig. 4). These are outpocketings, or diverticula, from the sides of the pharynx. Lateral to these pouches are corresponding invaginations from the external surface of the animal, known as branchial grooves. Due to the difference in origin, the pharyngeal pouches are lined with endoderm and the branchial grooves with ectoderm. The deepening of both internal and external pockets continues until their walls meet, forming a separating plate consisting of both endoderm and ectoderm. In aquatic vertebrates, this plate breaks through, establishing communication between the cavity of the pharynx and the external environment. These are the gill slits, the inner portion of which is lined with endoderm, the outer with ectoderm. The region between adjoining gill slits, consisting of muscles, integument, and other tissues supported by a branchial arch, is known as a gill septum.

In the fishes, the respiratory membranes, or gill filaments, develop from the inner walls of the gill slits. There is difference of opinion as to whether these membranes are ectodermal or endodermal in their origin. In the larval stages of the amphibians, gills develop from the epidermis. These are known as external gills as they are outside the gill slits. In certain salamanders, such as *Necturus*, two gill slits persist, as do the gills, throughout life. In others, as in *Cryptobranchus*, only one gill slit breaks through, and gills are functional during larval life only. In the adults of higher salamanders and of frogs and toads, there are no gill slits. The gills, which are functional during the larval stages, are external as far as their origin is concerned, but in some cases have been partially covered over by folds of integument for greater protection. In the adult in most cases these gills are lost and respiration becomes pulmonary and cutaneous.

In reptiles, birds, and mammals, the allantois functions as the embryonic respiratory membrane. Gills are never present in these terrestrial vertebrates, but pharyngeal pouches and branchial grooves appear, and, in modified form, portions of the pouches persist as various structures not concerned with respiration. Gill slits normally break through in reptiles and birds but do not persist in the adult. The eustachian tube and the cavity of the middle ear develop from the first pharyngeal pouch. Other pharyngeal pouches contribute to the formation of various ductless glands to be described later (Fig. 395).

The lungs, which become the respiratory organs of the adult in most amphibians, the reptiles, the birds, and the mammals, are also derived from the anterior part of the alimentary canal. The lung first appears as a fingerlike diverticulum (Fig. 280) pushing out from the ventral floor of the posterior region of the pharynx. This later subdivides, forming a bilobed sac. As development continues, the division becomes more definite, giving rise to the future lungs. The common duct formed by the extension of the lungs is the trachea. This branches, forming the two bronchi leading to the right and left lungs. The lungs may be further subdivided into smaller lobes, with branches of the bronchi, known as bronchioles, leading to them. The lobes of the mammalian lungs are subdivided into a series of small cavities, the alveoli.

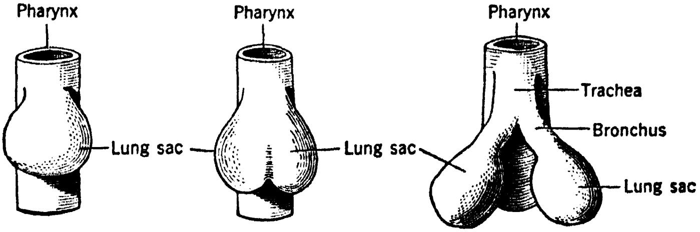


Fig. 280. Diagrams showing the development of the lungs. (From Wiedersheim, *Comparative Anatomy of Vertebrates*, by permission of The Macmillan Company, publishers.)

COMPARATIVE ANATOMY OF RESPIRATORY ORGANS

In describing the organs of respiration and the accessory structures characteristic of the different vertebrate classes, we shall begin in each case with those concerned with the intake of the respiratory medium (water or air).

CYCLOSTOMES. In *Petromyzon*, water may enter through the mouth or the gill slits. The pharynx is subdivided so that the dorsal or alimentary portion, the esophagus, is separated from the ventral or respiratory portion, the respiratory tube. The entrance to the latter tube is protected by a transverse membrane, the velum. In *Petromyzon*, as in most other aquatic vertebrates, the nasal cavity is not concerned with respiration, and does not communicate with the pharynx. The gill slits, which vary in number from six to fourteen pairs, widen out into separate pockets connected with the pharynx and with the external surface by narrow ducts. The gills are located within these pockets. In *Myxine* the nasal cavity communicates with the pharynx and the nasal opening serves as an entrance for the respiratory medium. The gill sacs do

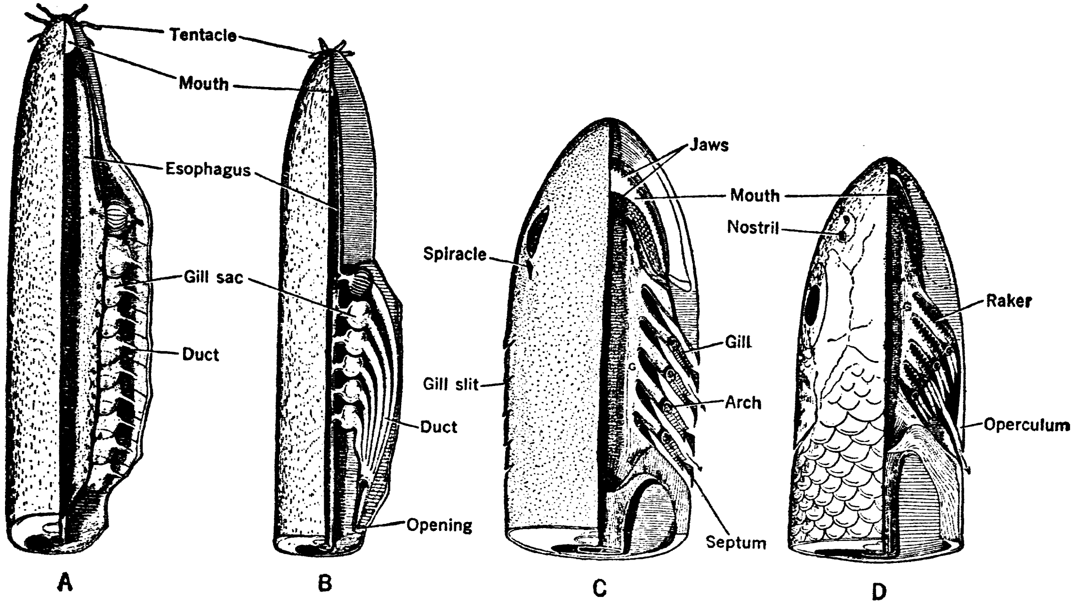


Fig. 281. Diagrams of heads showing respiratory organs. A, *Bdellostoma;* B, *Myxine;* C, a selachian; D, a teleost. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Dean, by permission of The Macmillan Company, publishers.)

not open separately to the outside, but lead posteriorly to a common (Fig. 281) opening.

CARTILAGINOUS FISHES. The water enters the mouth or the spiracle in these forms and passes out through the gill slits (Fig. 281 C), bathing the respiratory membranes which are the gill filaments. The paired gill slits vary in number from seven in the primitive shark, *Heptanchus*, to five, the number typical of most elasmobranchs. In addition to these, a modified gill slit, the spiracle, is characteristic of the class. This is located anterior to the other slits, developing between the mandibular and the hyoid arch. In the skates and rays, the spiracles open dorsally, with the true gill slits opening ventrally. The spiracles are not provided with functional gills, but may serve as an additional inlet for the respiratory medium. In the Elasmobranchii the gill slits open directly to the outside, while in the Holocephali, they are partially covered by a flap of integument, the operculum. Between the gill slits are wide septa supported by arches. On both walls of each septum are the gill filaments, each known as a hemibranch.

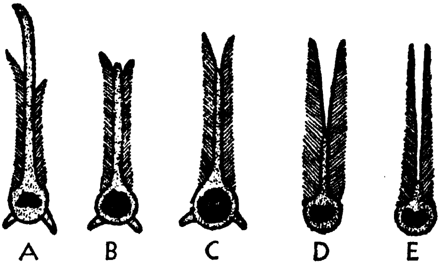


Fig. 282. The progressive reduction of gill septa in different fishes. A, elasmobranch; B, holocephalan; C, ganoid; D and E, teleosts. (From Walter, *Biology of the Vertebrates*, after Boaz, by permission of The Macmillan Company, publishers.)

THE BONY FISHES. The essential differences in the respiratory system of these fishes as compared with that of the elasmobranchs are the reduction in the number of slits, the progressive reduction of the size of the gill septa (Fig. 282), and the greater development of the operculum (Fig. 281D). The number of gill slits is typically five pairs, while in some teleosts only two are preserved. Spiracles are not typical but are present in such forms as the sturgeons. The septa practically disappear in the higher teleosts, so that the hemibranchs no longer lie in separate chambers.

Another structure characteristic of teleostomous fishes should be mentioned here, since in several forms it is modified in such a way as to form an efficient respiratory organ. This is the air bladder, a thin-walled sac which is derived as an evagination from the wall of the pharynx, probably from one of the more posterior pharyngeal pouches (Fig. 283). From its origin it grows backward until it occupies a great part of the dorsal portion of the coelom. In some fishes communication is retained with the pharynx by way of the pneumatic duct. In others this duct disappears. The function of the air bladder is primarily that of a hydrostatic organ. By changes in the volume of gases within the sac, the fish is able to maintain its position in different depths of water with a minimum of effort. The actual change of position, that is, to different levels and therefore to different pressures, is accomplished by movement of the fins. A structure known as the red gland, within the walls of the bladder, has the property of liberating free oxygen from the blood as it passes through the capillaries within (Fig. 284). Such oxygen may be returned to the blood stream through another network of capillaries (rete mirabile) in the wall of the sac, or liberated through the pneumatic duct when such a structure remains.

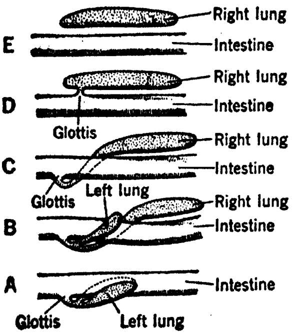


Fig. 283. Diagrams illustrating the lungs (air bladder), in fishes. A, primitive arrangement; B, *Polypterus;* C, *Ceratodus;* D, physostomous teleost; E, physoclistous teleost. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Kerr, by permission of The Macmillan Company, publishers.)

In *Polypterus*, the air bladder is bilobed, and its cavity is subdivided into smaller spaces, with the result that the internal surface is greatly increased. These structures resemble the lungs of higher forms also in their relation to the circulatory system. Their blood supply is furnished by pulmonary arteries, which are branches of the sixth pair of aortic arches.

DIPNOAN FISHES. The lungfishes possess gill slits and gills as well as lungs. Spiracles are present in the embryo but disappear in the adult. In *Protopterus*, external gills are present in addition to the pharyngeal gills. The lungs of these three forms are fundamentally very similar to those of terrestrial vertebrates. Offering a relatively large surface and being plentifully supplied with capillaries, they have the appearance of more efficient organs of respiration than the simple saccular lungs of many of the amphibians.

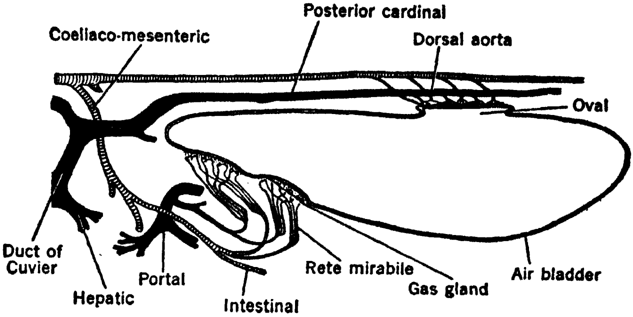


Fig. 284. Diagram of swim bladder of physoclistous teleost, showing blood supply. Left side view. Veins black, arteries cross-lined. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

During the dry seasons of the year, *Lepidosiren* of South America, and the African lungfish, *Protopterus*, bury themselves in the mud and are able to live in this condition for several months. When water is plentiful they come to the surface frequently for the purpose of gulping air. *Neoceratodus*, the Australian lungfish, apparently does not aestivate during the dry season, but, like the other members of this order, comes to the surface for air.

There is much difference of opinion among biologists concerning the relation of the air bladder to the lung. Some hold that they are homologous structures, the lung being derived by modification and specialization of the air bladder. Others are of the opinion that the functional lung appeared first but lost its respiratory function and took on that of a hydrostatic organ, as in most teleost fishes. Still others seem to think that the two structures developed independently to serve two fundamentally different functions. A study of the embryology of the two organs indicates that they are homologous structures.

AMPHIBIANS. It was stated above that the larval amphibians are equipped with external gills of epidermal origin. These persist in the adult in such permanently aquatic forms as *Necturus*. Although gill slits remain, they apparently do not serve their original purpose, since the external gills are constantly in motion in the water, from which they take fresh supplies of oxygen.

The absence of both gills and lungs in the adult plethodontid salamanders has been previously mentioned. In these forms respiration is integumental and pharyngo-esophageal.

Lungs are present in all other amphibians and, with the exception of *Necturus* and a few related species, the pulmonary-cutaneous method of respiration has entirely taken the place of the branchial. The air route is by way of the external nares through the nasal chambers, and then by way of the internal nares into the mouth cavity (Fig. 44). In the mouth cavity or in the pharynx, of all the terrestrial vertebrates, the respiratory route crosses the food route (Fig. 267), as described in the preceding chapter. An opening from the floor of the pharynx, the glottis, leads to the trachea, a tube leading to the lungs. The trachea is short in the amphibians, especially in the salamanders, leading almost directly into the lungs. A division of the trachea, forming two short tubes, the bronchi, which lead to the lungs, appears in some amphibians.

Associated with the anterior end of the trachea in terrestrial vertebrates is a series of cartilages and muscles, which form the larynx. This structure is very simple in the salamanders (Fig. 285) where it appears for the first time. In *Necturus*, it consists of a pair of small cartilages known as laterals, on either side of the glottis. In *Proteus*, these are more extensive and in the adult are divided into two cartilages, the anterior and dorsal arytenoids and the posterior ring-shaped cricoid. A study of the development of the lateral cartilages shows that they were derived from portions of the fifth branchial arches of the fishes. In the higher classes, with the elongation of the trachea, it is encircled by a series of tracheal rings. These also have been traced from the fifth arch.

The larynx is associated not only with regulating the intake and outgo of air, but also with the production of sound. In the Salientia for the first time we find vocal cords located within the larynx. These structures may be set into vibration as air is forced through the tube, producing sounds characteristic of the species. The male frog is also provided with paired vocal sacs which open from the pharynx. These act as resonance chambers which increase the range of the sounds produced. In the tree frogs and many of the toads a single median vocal sac is present.

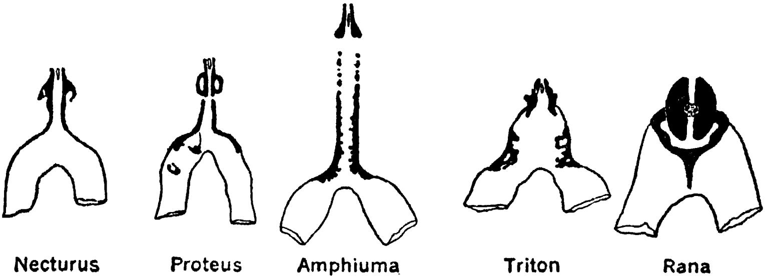


Fig. 285. Laryngeal cartilages of various amphibians. (From Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

In the frog the arytenoids are large semielliptical plates at the sides of the glottis. The cricoid consists of a ventral Y-shaped cartilage, the sides of which are lateral to the arytenoids; and a dorsal U-shaped portion with a pair of processes projecting posteriorly.

The lungs of the amphibians are rather simple, thin-walled sacs with few modifications for the increase of the internal surface (Fig. 286). In *Necturus* they are long and slender and play a very minor role in respiration. In frogs and toads they are more spherical, and internal folds projecting from the walls increase somewhat the total area of the respiratory membrane.

The importance of the amphibian integument as an organ of respiration has been mentioned previously. The skin is richly supplied with capillaries which branch from a large blood vessel, the cutaneous branch of the pulmocutaneous artery. Moistened by the secretion of numerous glands, it makes an extensive and efficient membrane for the exchange of gases between the respiratory and circulatory media.

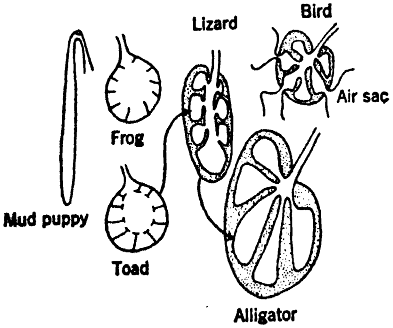


Fig. 286. Diagrams to show the evolution of lung structure. (Redrawn from Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

REPTILES. Because of the presence of the allantois, the reptilian embryo has no need of gills or gill slits. Remnants of portions of the branchial apparatus, such as pharyngeal pouches and branchial grooves, are present. The first three pairs may break through to form temporary gill slits.

The anterior portion of the air passage is essentially similar to that of the amphibians, except that the development of a hard palate has carried the internal nares backward so that the crossing of the respiratory and alimentary routes is in the posterior part of the pharynx. Important advances are seen, however, in the larynx and trachea. Arytenoid, cricoid, and tracheal cartilages are present. The trachea is long in reptiles generally, and is kept from collapsing by the numerous tracheal cartilages, which in this class are in the form of complete rings. The anterior tracheal cartilages have given rise to a large cartilage, the cricoid. The trachea divides into bronchioles leading to the ultimate divisions of the lungs.

The reptile lung shows a high degree of specialization as compared with that of the amphibians. The area of the inner surface is greatly increased by numerous partitions growing out as folds from the endodermal walls. In most snakes, the left lung is absent. In some lizards the lungs are supplemented by numerous tubular diverticula from their outer surfaces (Fig. 287). In the crocodilians the lungs approach the mammalian condition, their cavities being subdivided, forming numerous small chambers, the alveoli.

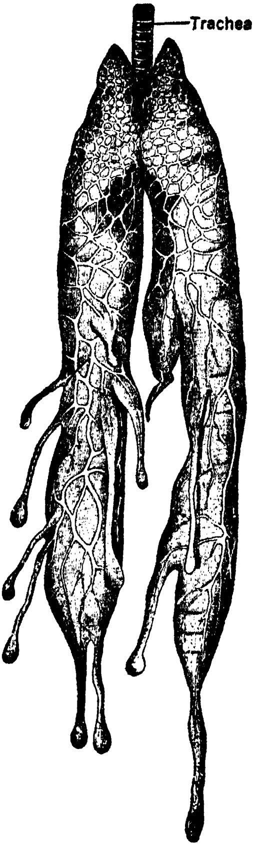


Fig. 287. The lungs of a lizard, *Chamaeleo monachus*, showing the accessory lobules. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Wiedersheim, by permission of The Macmillan Company, publishers.)

BIRDS. Four pairs of pharyngeal pouches and branchial grooves are present in the embryo. As in the reptiles, with the exception of the first three pairs, these do not normally break through. The trachea is a very long tube supported by complete tracheal rings. In some birds the trachea is longer than the neck and, therefore, becomes looped. In the swan the loop is tucked away in a cavity of the sternum. The larynx of birds is rather poorly developed, but a so-called secondary larynx, the syrinx (Fig. 288), is located at the opposite end of the trachea, where this tube divides to form the bronchi. The arytenoids are slender curved cartilages in which some ossification has taken place. The cricoid is in two parts, a triangular portion on the ventral side of the larynx and a dorsal median cartilage between the ends of the arytenoids. This is known as the procricoid. The syrinx is formed by modification of tracheal and bronchial rings and serves as the voice box of the bird. A vibrating bony ridge, the pessulus, and internal folds or membranes take the place of the vocal cords of other vertebrates in the production of sound.

The lungs of birds are modified by the addition of supplementary air sacs (Fig. 75). Growing out from the ventral surface of the lungs, these sacs extend into the body cavity and occupy available spaces between the viscera and muscles and within the hollow bones. Although not in themselves forming respiratory membranes, these additional sacs take part in the respiratory process by aiding in the circulation of air through the air capillaries. The exchange of gases takes place as the air passes through the alveoli in either direction, toward the accessory sacs or from them. They also serve the purpose of making the body of the bird lighter while in the air.

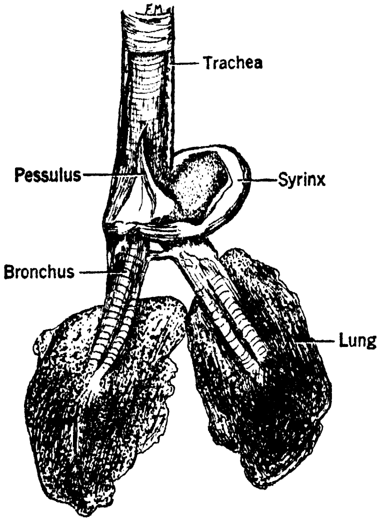


Fig. 288. Dissection of the syrinx of the duck.

MAMMALS. The anterior portion of the respiratory system of the mammals is not essentially different from that of the birds. The extensive nasal chamber is lined with mucous membrane richly supplied with capillaries. Thin plates of bone, the turbinals, growing out from surrounding bones of the skull, not only increase the surface but prevent the entrance of dust and other injurious particles. The air pathway crosses the food pathway far back in the laryngopharynx (Fig. 267).

Four pairs of pharyngeal pouches and branchial grooves are present in the embryo, but they do not normally break through. The first pouch, as in the birds and reptiles, forms the eustachian tube and the cavity of the middle ear. The larynx of mammals (Fig. 289) is more highly developed than that of the preceding classes. Additional cartilages which develop from remains of other branchial arches become associated with this anterior portion of the trachea. The formation of the arytenoid, cricoid, and tracheal cartilages from the fifth branchial arches was noted in the preceding classes. A large cartilage, the thyroid (Fig. 290), located anterior to the cricoid, is also characteristic. This is derived from the fourth and fifth branchial arches, according to evidence furnished by the monotremes. In this order there are two separate thyroid cartilages which apparently have that origin. Portions of the hyoid bone are attached to the larynx by ligaments.

The epiglottis is a rounded structure supported by fibrocartilage, which protects the glottis. It is ventral to the glottis and folds back over it like a lid when the food is being swallowed. It was formerly believed that its cartilage represented parts of the fourth branchial arch but this is now considered somewhat doubtful.

The vocal cords (Fig. 291), which are highly developed in mammals, consist of two pairs of folds of elastic fibers, extending from the arytenoid cartilages to the thyroid cartilage. Their position and tension is regulated by muscles.

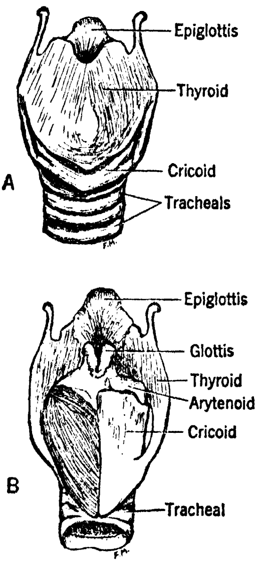


Fig. 289. The larynx of the cow, showing cartilages. A, ventral; B, dorsal (muscles of the right side removed).

The trachea of mammals is usually straight and its length determined by that of the neck. *Bradypus*, the three-toed sloth, is a notable exception, for its trachea forms an extended loop in the thorax before entering the lung. The tracheal rings, with few exceptions, are incomplete dorsally. In the water-living carnivores, they are complete rings, and in the Cetacea, incomplete ventrally.

The trachea usually divides, forming two bronchi. In the whales, the pigs, and some ruminants, three bronchi are present. The bronchi subdivide into numerous bronchioles which lead to the functional units of the lungs, the alveoli. The mammalian lung differs from that of other vertebrates in being divided into several lobes. The lungs are asymmetrical in this respect, there being usually more lobes on the right side than on the left. In many, for example, there are three lobes in the right lung and two in the left. In the rat (Fig. 292), there are four in the right lung, while the left, as in the monotremes, is undivided. In many ungulates and in the aquatic orders (Cetacea and Sirenia) both sides are undivided.

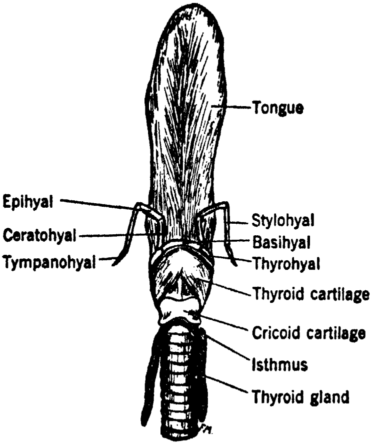


Fig. 290. The larynx of the cat (ventral view), showing the hyoid bones and the tongue.

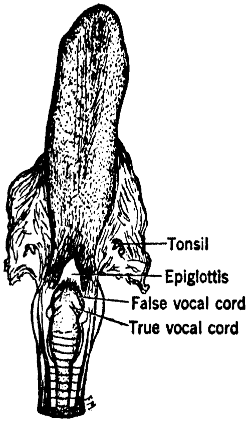


Fig. 291. The larynx of the cat (dorsal view), dissected to show the vocal cords.

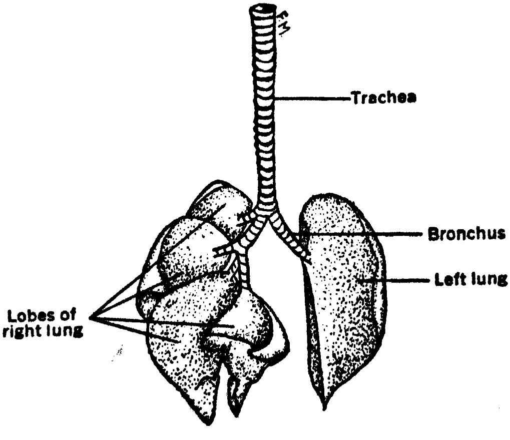


Fig. 292. Lungs of the white rat, showing lobes, and divisions of the right bronchus.

ACCESSORY STRUCTURES

It was stated above that in addition to the main organs of respiration, a variety of other structures play an important part in the respiratory process. These may be divided into two main groups, those concerned with the protection of the delicate membranes, and those which aid in providing a continuous current of the respiratory medium. Among the protective structures may be mentioned the operculum and the gill rakers of fishes, the glands of the amphibian skin, and the turbinal bones and protective hairs of the nasal chamber of mammals. In the alligator, the velum forms a curtain that shuts off the internal nares from the mouth cavity, making it possible for the animal to breathe under water, even with the mouth open, as long as the external nares are out of water. The epiglottis of mammals, guarding the entrance to the trachea, has already been described.

In fishes the flow of water over the gill filaments is produced by muscular movements, and a series of valves prevents a flow in the wrong direction. There are typically two sets of these valves, an anterior group along the inner edge of the mouth opening and a posterior set (branchiostegal) along the outer margins of the operculum. Muscular movements of the walls of the mouth and pharyngeal cavities produce the current of water, while the alternate opening and closing of the two sets of valves determine its direction (Fig. 293). In some elasmobranchs, the spiracle is substituted for the mouth as the respiratory doorway.

In the larval amphibians, the external gills are in constant movement in the medium itself. In the adult frog, valves associated with the external nares serve a purpose similar to those described above in the fishes, while movements of the medium (air) are produced by the alternate contraction of throat and body muscles.

Among the reptiles, the turtles use the amphibian combination of nasal valves and throat muscles. In other reptiles, the rib muscles play an important part in pulling air into and out of the lungs.

When the bird flies, the action of the pectoral muscles keeps a current of air moving in and out of the air sacs. When the bird is not in flight, the intercostal muscles act much as they do in most reptiles.

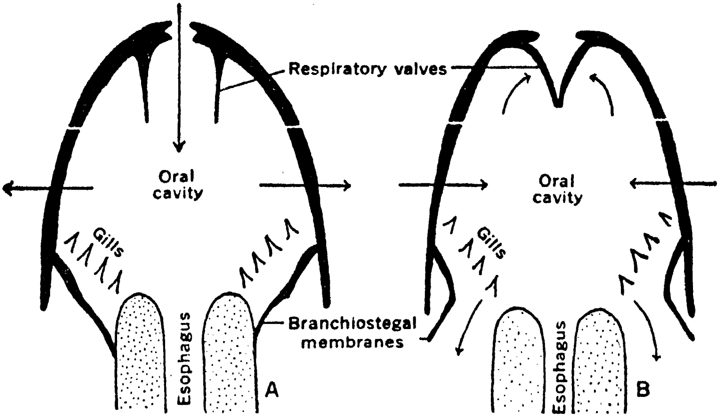


Fig. 293. Diagrams showing respiration in teleosts. A, inspiration; B, expiration. In both figures the anterior oral part represents a vertical section, and the posterior pharyngeal part a horizontal section. (Modified from Goodrich, *Studies in the Structure and Development of Vertebrates*, after Dahlgren, by permission of The Macmillan Company, publishers.)

SUMMARY

The respiratory system consists of those organs which bring oxygen to the blood stream and which provide for the elimination of the gaseous waste products of metabolism. The essentials of a respiratory system are a thin moist membrane, with oxygen on one side and blood on the other.

The chief vertebrate respiratory organs are gills and lungs. The former are characteristic of the cyclostomes, fishes, and larval amphibians, while the latter are found in the adult amphibians, reptiles, birds, and mammals.

In all vertebrate embryos lateral evaginations form in the wall of the pharynx. In aquatic forms these meet with invaginations from the outside, and the intervening walls break through forming gill slits. Gills develop along the inner walls of the gill slits. In reptiles, birds, and mammals the allantois functions as the respiratory membrane of the embryo. The lungs develop from the floor of the posterior region of the pharynx in the form of an evagination which later forms a bilobed sac. From these sacs the adult lungs are differentiated.

In typical aquatic forms water enters the mouth and passes out over the gill filaments through the gill slits. The gill slits are more numerous in the elasmobranch fishes than in the other groups and the septa between them are wider. In fishes above the elasmobranchs the gills are covered by an operculum and the septa almost disappear. The air bladder, a hydrostatic organ in most fishes, in some forms is modified to function as a respiratory organ.

In the amphibians gills are functional in the larval stages and lungs in the adult (except in such forms as the Plethodontids). The external nares are the entrance for the respiratory medium, the air. The respiratory route crosses the food route in the mouth cavity. The beginnings of the development of a voice box, the larynx, occurs in the salamanders, in the form of simple cartilages at the sides of the glottis. These are derived from the fifth branchial arches. In the Salientia vocal cords are present for the first time. The lungs are relatively simple, thin-walled sacs, with some modifications of internal structure in the frogs and toads, to increase the area of the respiratory membrane. The skin also serves as an important organ of respiration in this class.

There are no gills in the reptiles, although gill slits may appear in embryonic life. The beginnings of a hard palate and the greater development of laryngeal cartilages are characteristic. The reptilian lung is a more efficient organ than that of the amphibians and in some lizards is supplemented by tubular sacs.

In the birds the trachea is long and supported by numerous tracheal rings. A so-called secondary larynx, the syrinx, is present at the posterior end of the trachea. The lungs are highly efficient organs and are in communication with various accessory air sacs, which greatly increase their capacity.

The mammalian respiratory system is characterized by the posterior location of the internal nares, the development of an epiglottis guarding the entrance to the trachea, the greater development of the larynx and the vocal cords, and the increased efficiency of the lungs.

In addition to the essential parts of a respiratory system, there are usually present various other structures concerned with the protection of the membranes or with providing a continuous flow of the oxygen in one direction and wastes in the other.

XI. The Circulatory System

In the description of the digestive and respiratory systems reference was made to the blood as the medium of distribution of prepared food materials and of oxygen to the tissues of the body. The blood also transports waste materials, resulting from the various activities of the living organism, to those organs concerned with their elimination. Such organs make up the excretory system which will be described in a subsequent chapter. Again, the secretions of the ductless glands are carried throughout the body by the blood stream. The blood, therefore, may be considered to be the common carrier of the body. Together with the series of tubular vessels through which it flows, it constitutes the circulatory system.

PARTS OF THE SYSTEM

The vertebrate circulatory system consists of the blood and the definite network of closed vessels through which it flows, and of the lymph and its less definite system of vessels, the lymphatics. The parts of the system will be described before considering their development.

The Blood

The blood is a red fluid consisting of a liquid portion, the plasma, and of various solid bodies, the cells. The plasma consists of about eighty per cent water, in which are dissolved various substances being distributed throughout the body. Among these may be mentioned various gases such as oxygen, nitrogen, and carbon dioxide; food stuffs such as proteins, fats, and carbohydrates; waste materials such as urea and uric acid; mineral salts, particularly sodium chloride; secretions of the ductless glands; and such protective substances as opsonins, agglutinins, and antibodies in general.

The blood cells, or corpuscles, are of two main types, the red cells or erythrocytes, and the white cells or leucocytes. The erythrocytes are typically flattened cells, oval or elliptical in shape, with definite rounded nuclei. In mammals (Fig. 294), however, these cells are more circular in outline, are biconcave, and, when fully developed, are without nuclei. The size of the erythrocytes is subject to much variation among the vertebrates. The largest described are those of *Amphiuma*, which measure seventy-five micra (75/1000 of a millimeter), while the smallest are found in *Tragulus*, the musk deer, and measure only two and one-half micra. In man, the diameter is approximately seven and one-half micra. In general, it may be stated that the erythrocytes of the lower and cold-blooded vertebrates are larger than those of the more active and warm-blooded classes.

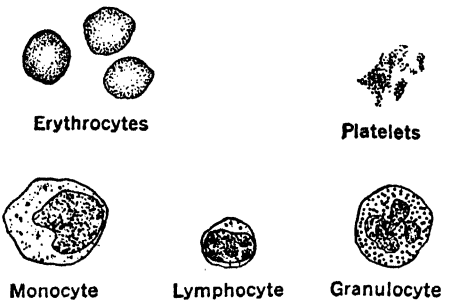


Fig. 294. Mammalian blood cells. (Prepared and drawn by Belle Berkowitz.)

The chief function of the erythrocytes is to distribute oxygen. Haemoglobin, the chemical pigment to which the characteristic color of these cells is due, has the property of readily forming a combination with large quantities of oxygen, producing oxyhaemoglobin. This combination is just as readily broken down and, as a result, oxygen is liberated to the tissue cells where needed.

The white blood corpuscles, or leucocytes, may be classified into three general types, lymphocytes, granulocytes, and monocytes (Fig. 294). The lymphocytes occur in various sizes, are more or less spherical, and each cell has a single nucleus. In the granulocytes, as the name implies, the cytoplasm is granular. They are larger than the lymphocytes, and their nuclei appear in a variety of shapes. Consequently they are often known as polymorphonuclear leucocytes. These cells remove worn-out tissue cells and also destroy bacteria by surrounding and digesting them in an amoebalike manner. When engaged in such desirable labors, they are known as phagocytes. They are able to force themselves between the cells which form the capillary walls, thereby escaping from the blood stream into the intercellular spaces. The escape of leucocytes from the capillaries, which is known as diapedesis (Fig. 295), makes possible their phagocytic activities among the cells of the various body tissues. They are subsequently returned to the blood stream by way of the lymphatic vessels. Monocytes are large leucocytes containing a single large nucleus. They constitute a very small proportion of the entire number of leucocytes.

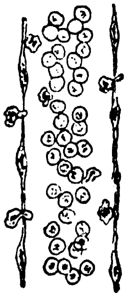


Fig. 295. Diapedesis of leucocytes. (From Walter, *Biology of the Vertebrates*, after Burton-Opitz, by permission of The Macmillan Company, publishers.)

In addition to the red and white corpuscles, other less definite bodies are present in the blood. These are usually known as thrombocytes. In the lower vertebrates such bodies are often referred to as spindle cells, while in the mammals they are called blood platelets. These various bodies take part in the formation of the blood clot which prevents excessive bleeding from a wound.

Blood Vessels

The closed system of vessels through which the blood circulates includes the heart, arteries, veins, and capillaries (Figs. 296–298). The heart may be considered to be the central pumping station, the contraction of its muscular walls causing blood to be forced from it through the narrow vessels. It consists of two or more communicating chambers, partially separated by internal septa. Leading out from the heart are the arteries, which repeatedly subdivide, forming smaller branches leading to the various organs of the body. Within

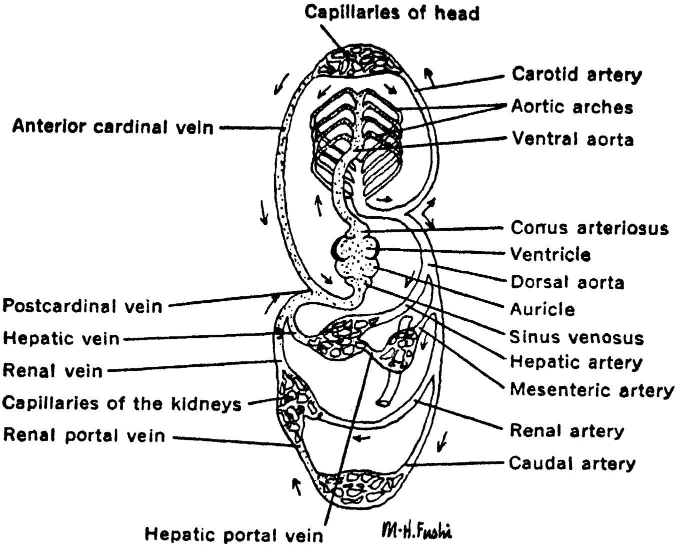


Fig. 296. Plan of the vascular system of a fish. Arterial blood, unshaded; venous blood, shaded. Arrows indicate direction of blood flow. (Redrawn from Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

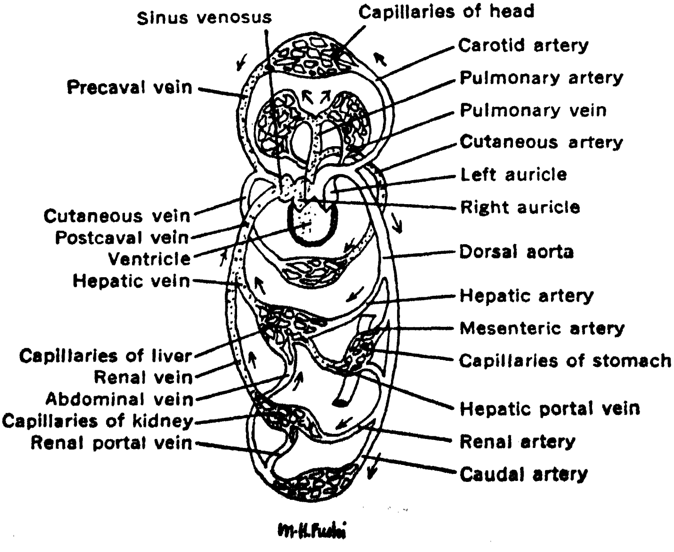


Fig. 297. Plan of the vascular system of an amphibian. Arterial blood, unshaded; venous blood, shaded. Arrows indicate direction of the blood flow. (Redrawn from Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

the organs, the arteries continue to branch, eventually becoming minute tubes, the capillaries. Numerous capillaries unite to form larger vessels, the veins, which later unite with similar vessels from other organs to form larger veins which empty into the heart. The arteries, therefore, carry blood away from the heart; while the veins return it to that organ. Capillaries are the narrowest portions of this series of tubes. They connect arteries and veins as described above, and also, in certain parts of the system (portals), may connect two veins.

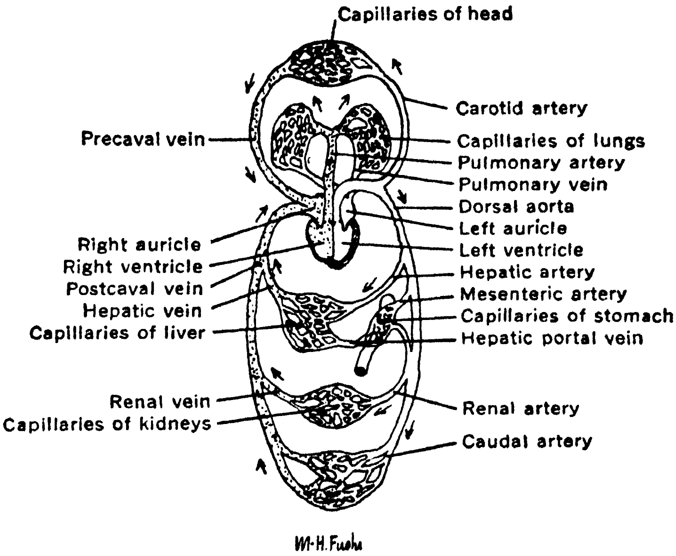


Fig. 298. Plan of the vascular system of a mammal. Arterial blood, unshaded; venous blood, shaded. Arrows indicate direction of blood flow. (Redrawn from Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

When seen in cross section, the blood vessels consist of three layers: an inner layer of epithelial cells, the endothelium; an outer layer of connective tissue; and a middle layer of circular (smooth) muscles. The relative importance of these layers varies in the different vessels (Fig. 299). In the larger arteries the muscle layer is prominent, while in the veins it is less well developed. The outer layer also is thinner in the veins, and the fibers are more loosely arranged. The capillaries consist almost entirely of the endothelial layer.

The Lymph

The lymph is a thin, watery fluid surrounding the individual cells of the body. It is derived from that portion of the blood which passes through the walls of the capillaries, and ultimately is returned to the blood by way of the lymphatics. It is by way of the lymph that the cells obtain food, and into it their wastes are discharged. The lymph also contains leucocytes which have passed through the capillary walls as described above.

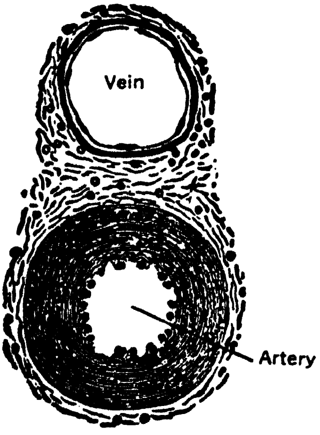


Fig. 299. Cross section through a small artery and a small vein, showing the relative difference in the thickness of their walls. (From Mavor, *General Biology*, after Kimber, Gray, and Stackpole, by permission of The Macmillan Company, publishers.)

Lymph Vessels

The lymphatics begin in the small and rather indefinite spaces found between adjoining cells. From these intercellular channels more definite tubules, with thin and delicate walls, lead to larger vessels having stronger walls supported by connective tissue (Fig. 300). The lymphatics leading from the walls of the intestine are known as lacteals. All these eventually lead into the largest lymph vessels, the lymphatic ducts which empty directly into the blood vessels at definite places. The larger cavities of the body, such as the pleural, peritoneal, and pericardial, also belong to this system. The lymph in these cavities drains into the lymphatics through small openings in their membranous linings.

Along the course of the lymphatics are solid glandular bodies known as lymph nodes (Fig. 301). These glands contain small amoeboid cells known as lymph corpuscles or lymphocytes. Lymphatics leading into and away from these nodes are known as afferent and efferent vessels, respectively. Among larger lymph organs of a similar character may be mentioned the spleen, the tonsils, and the thymus gland.

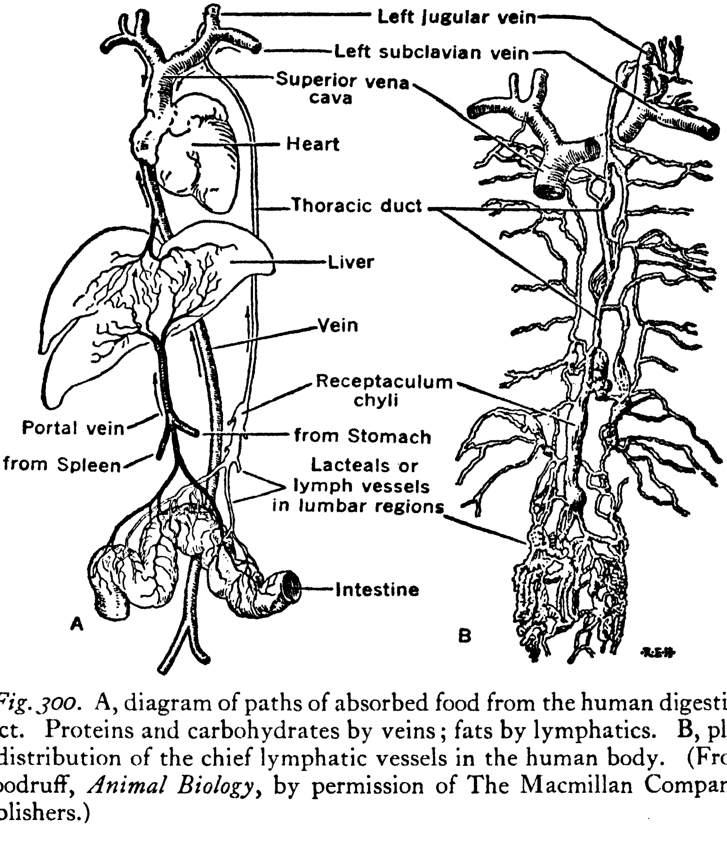


Fig. 300. A, diagram of paths of absorbed food from the human digestive tract. Proteins and carbohydrates by veins; fats by lymphatics. B, plan of distribution of the chief lymphatic vessels in the human body. (From Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

EMBRYOLOGY OF THE CIRCULATORY SYSTEM

The development of the circulatory system of a higher vertebrate recapitulates to a surprising degree its evolutionary development through the various classes. The change from a water to an air environment, as we have previously seen, brought about a profound change in the respiratory system. This was necessarily accompanied by a correspondingly significant modification of the circulatory system. In the amphibians, that class in which this change in environment actually takes place, it is to be expected that the circulatory system of the embryo would be of the branchial type and that of the adult of the pulmonary type. That a similar change is seen during the development of the embryo in the reptiles, birds, and mammals, all terrestrial forms in which branchial respiration is at no time employed, is a striking and most significant fact.

Although there is much variation in details in the early stages of development in the different vertebrate classes, it is possible to describe the more important changes in fairly general terms. The embryo of higher vertebrates is first seen as a circular and rapidly multiplying disc of cells on the surface of a spherical body of yolk. As long as it consists of a layer of cells, the embryo draws its nourishment directly from the yolk. As the body increases in size with the formation of several layers of cells, portions of the embryo become far removed from the surface of the yolk. It is necessary, therefore, that some provision be made for the transportation of food materials from their source in the yolk to outlying regions of the embryo.

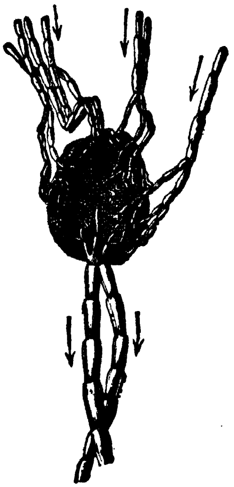


Fig. 301. A lymph node, with its afferent and efferent vessels. (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, after Gerrish, by permission of The Macmillan Company, publishers.)

Groups of mesenchyme cells become differentiated around the edge of the embryo, forming so-called blood islands. These consist of haemopoietic, or blood-forming, cells and endothelial cells, which later form the linings of the blood vessels. These islands next form a network of capillaries on the surface of the yolk, from which emerge a pair of definite vessels, the vitelline veins, which lead directly into the developing embryo.

Meanwhile, similar capillary networks within the embryo are forming, and, by the coalescence of neighboring portions of the network, the first definite system of blood vessels is formed. At an early stage this consists of a simple but complete circuit from the yolk sac to the embryo and back again (Fig. 302A). The vitelline veins enter the embryo, unite, and then continue anteriorly as the ventral aorta, from which the heart is eventually differentiated. Anteriorly, the ventral aorta divides, forming two vessels, the original aortic arches. These curve dorsally and then continue posteriorly along the middorsal region as the dorsal aortae. In the posterior region of the embryo, the dorsal aortae curve ventrally and then anteriorly to leave the embryo as the vitelline arteries, which pass through the yolk stalk. On the surface of the yolk sac the vitelline arteries branch repeatedly to communicate with the capillaries, in which the vitelline veins begin. The paired dorsal aortae later unite posterior to the pharyngeal region, forming a single dorsal aorta.

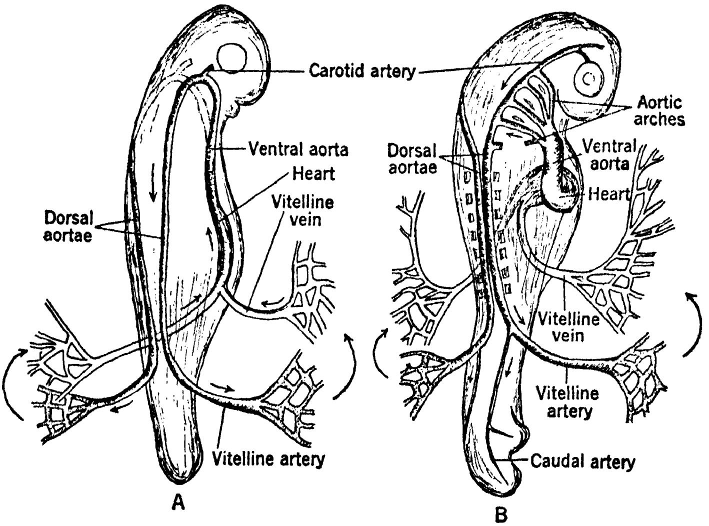


Fig. 302. Early circulation of vertebrate embryo. A, first appearance of definite vessels; B, later stage, during the formation of gill arteries. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

With the development of the functional respiratory organs in the pharyngeal region, additional aortic arches are formed connecting the ventral and dorsal aortae posterior to the first and original aortic loop (Fig. 302 B). In the fishes these remain in the adult as important parts of the circulatory system (Fig. 296). In this class they are subdivided by the capillaries of the gills into two parts, the afferent and efferent branchials. The afferent vessels lead to the gills; the efferents, away from them. In the larval amphibian also, the aortic arches are important vessels associated with the branchial system of respiration. In the adult amphibian, however, only portions of this part of the system remain. In the remaining vertebrate classes, although a series of complete aortic arches is present in the embryo, they are not concerned with respiration, since functional gills are never present.

As development of the embryo continues, and as the various organs and appendages are formed, it becomes necessary to supply these new structures with food materials. Consequently, a number of branch arteries arise from the simple system described above to carry blood to these organs. The carotid arteries leading from the more anterior aortic arches supply the important structures of the head region. The subclavians, supplying the anterior appendages, arise from the anterior part of the dorsal aorta in some classes; in others, from the ventral part of the aortic arches. Iliacs, branching from the dorsal aorta, supply the posterior limbs, while the caudal artery extends into the tail as a posterior continuation of the dorsal aorta.

These vessels branch into capillaries in these various organs. From these capillaries the blood is returned by a series of veins, which unite in the anterior part of the body to form a pair of large veins, the anterior cardinals. Similarly, a pair of posterior cardinals drain the posterior part of the body (Fig. 303). The anterior and posterior cardinals of each side unite to form the ducts of Cuvier, which empty into the posterior part of the heart.

With the development of the alimentary canal, in preparation for that time when it must replace the yolk sac as the source of nourishment for the growing organism, a number of important vessels develop. Arteries which arise from the dorsal aorta lead to the intestinal walls, where they form a

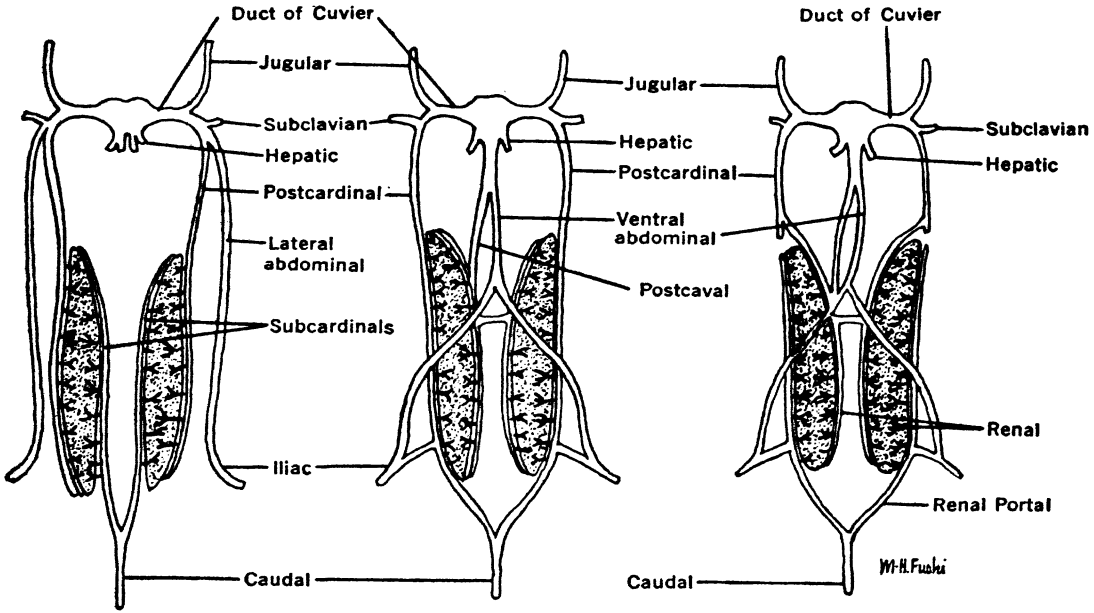


Fig. 303. Diagrams showing the relations and modifications of the postcardinal, subcardinal, abdominal and postcaval veins in different stages of the amphibians. (Redrawn from Kingsley, *Comparative Anatomy of Vertebrates*, The Blakiston Company, by permission of Miss Mary W. Kingsley.)

capillary network. From the capillary network numerous veins arise which unite to form a large vessel, the mesenteric or subintestinal. This communicates with the vitelline veins shortly after the latter reach the embryo. The large veins formed by the junction of vitellines and mesenteric are known as omphalomesenterics.

The development of the liver in this region influences the future history of these veins just posterior to the heart (Fig. 304). The liver forms around the omphalomesenteric veins, and that portion of them passing through this organ gives rise to the series of capillaries characteristic of the vertebrates. Portions of both veins leading into this capillary network take part in the formation of the hepatic portal vein, which drains the alimentary canal of the adult. The portions between the capillaries of the liver and the heart remain as hepatic veins.

When kidneys develop, a renal portal system is formed along the route of the postcardinals. The caudal vein from the tail divides in the region of the cloaca to form the two renal portal veins which give off numerous renals which lead to the capillaries of the kidneys. From the kidney capillaries, other renal veins empty into the postcardinals. The renal portal system becomes reduced in birds and disappears in mammals with the development of a different type of kidney.

In all vertebrates above the amphibians, the presence of the allantois also influences the development of the circulatory system. Since, as we have previously indicated, this is the important respiratory membrane of the embryo of terrestrial vertebrates, it must be connected to the embryonic circulatory system. This connection is by way of the allantoic arteries and veins. The allantoic arteries lead from the posterior part of the dorsal aorta to capillaries in the allantois. The allantoic veins return blood from these capillaries and enter the ventral aorta (heart) near the omphalomesenterics. In the mammals, the allantoic vessels are known as the umbilicals, and in the placental mammals they soon replace the vitelline veins as carriers of food materials.

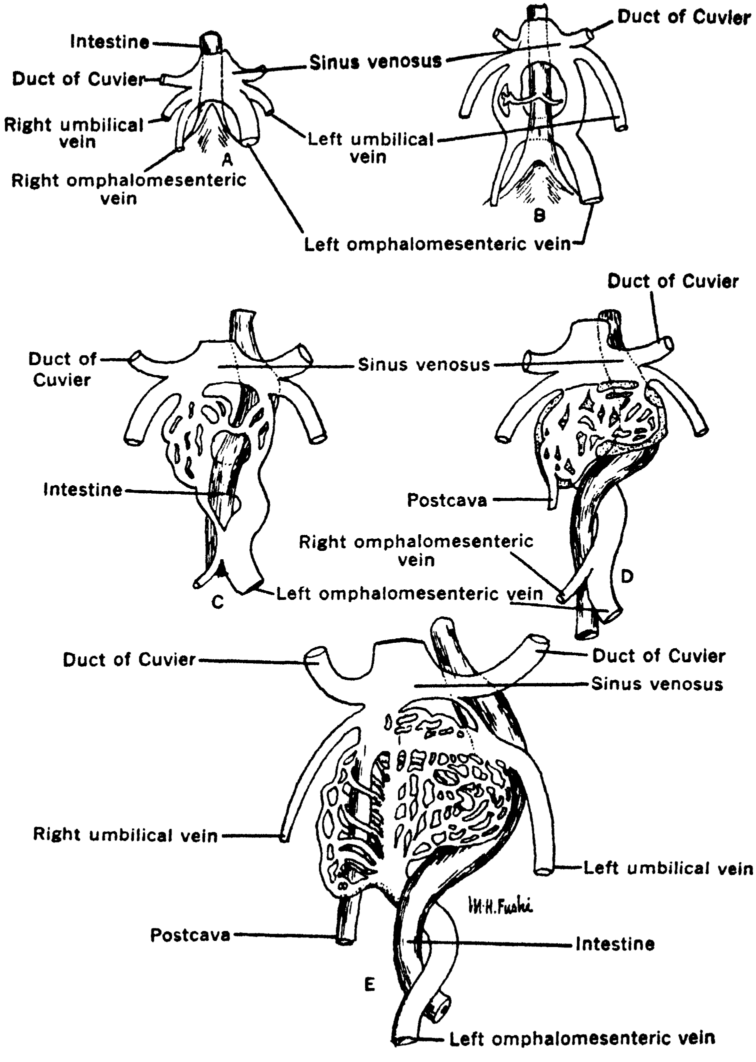


Fig. 304. Development of the postcava and the hepatic portal system in the lizard (*Lacerta*). The figures (A) to (E) represent consecutive stages of development. (Redrawn from Wilder, *The History of the Human Body*, after Hochstetter, by permission of Henry Holt and Company.)

THE HEART

The heart, the muscular pumping organ of the vertebrate circulatory system, is a modification of a tubular cavity, or a pair of them, lying in the ventral mesentery in the anterior part of the embryo. The tissues of the walls of the heart arise from the mesenchyme of the splanchnic mesoderm surrounding these cavities in the same way that the blood vessels form. In those cases where there are originally two cavities, these later come together and fuse. Among the changes which may be seen in the development of this organ in the vertebrates are local thickenings of the muscular layer, constrictions (Fig. 305), bendings, and the formation of internal longitudinal septa (Fig. 306).

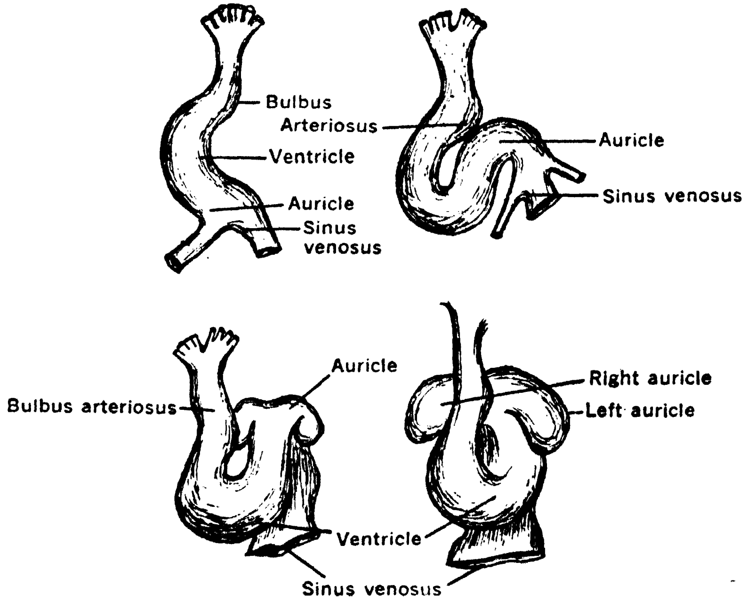


Fig. 305. Diagrams showing stages in the development of the heart. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

In an early stage of development the heart is still a straight tube. Later, with the lengthening of this tube in a restricted space, it is bent, forming an S-shaped structure. It then becomes divided by a series of constrictions into four partially separated chambers. These are, beginning posteriorly, the sinus venosus, the atrium, the ventricle, and the bulbus cordis. The veins empty into the sinus venosus, and the bulbus cordis (conus arteriosus) narrows and continues anteriorly as the ventral aorta. As a result of this bending, the atrium lies dorsal to the ventricle. The heart of the cyclostomes and of most fishes (Dipnoi excepted) represents this stage of the phylogeny of the organ.

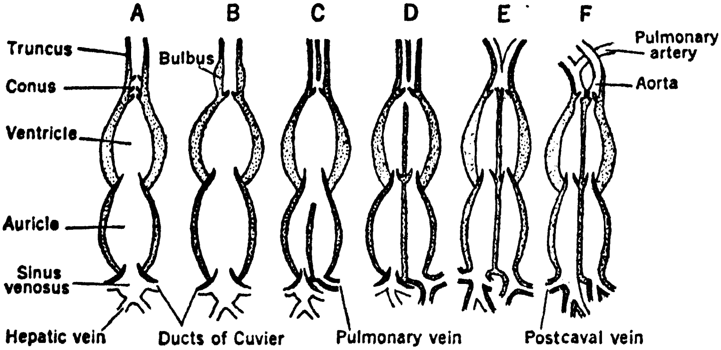


Fig. 306. Diagrams of the evolution of the heart. A, elasmobranchs; B, teleosts; C, amphibians; D, lower reptiles; E, alligators; F, birds and mammals. (Redrawn from Walter, *Biology of the Vertebrates*, after Kingsley, by permission of The Macmillan Company, publishers.)

The next important step is the formation of a longitudinal septum within the atrium (Fig. 306). When this is complete, as in the amphibians (practically so in the Dipnoi), the atrium is subdivided into two chambers, the right and left auricles. The systemic veins empty into the right auricle; the pulmonary veins, into the left. Both auricles open into the single ventricle, but due to the relation between the openings, to the action of various valves, and to the arrangement of the different openings which lead from the conus arteriosus into the various arteries branching from it, a partial separation of venous and arterial blood is accomplished.

In the reptiles, a further important modification is illustrated, namely, the greater development of the interventricular septum, traces of which appear in the Salientia. The septum is incomplete in all orders except the Loricata, so that the typical reptilian heart resembles that of the amphibians in general appearance. In the crocodilians the septum is complete except for an opening, the foramen of Panizza, between the base of the pulmonary artery and the beginning of the aortic arch.

The sinus venosus has become less important in this class of vertebrates and is eventually incorporated into the right auricle. The conus arteriosus also disappears with the complete separation of the right and left sides of the ventricle. This division results in the separation also of the large vessels which leave the ventricles, namely, the pulmonary arteries and the aortic arch.

In the birds and mammals, also, the interventricular septum is complete. This brings about a separation of the right and left sides of the heart, and consequently a separation within the heart of arterial and venous blood. The sinus venosus and the conus arteriosus are no longer present. The four-chambered heart of the higher vertebrates is thus formed by the subdivision of the two remaining parts of the fish heart, the atrium and the ventricle.

COMPARATIVE ANATOMY OF THE CIRCULATORY SYSTEM

As a starting point for a comparison of the general plans illustrated in the circulatory system of the different vertebrate classes, the system present in *Amphioxus* should be kept in mind.

Cyclostomes. The circulatory system of the cyclostomes is very similar to that of *Amphioxus*. The most noticeable advances are in the presence of red blood corpuscles and the development of a definite heart. The heart is an S-shaped organ consisting of two main chambers, an auricle and a ventricle, and a thin-walled sac, the sinus venosus. The sinus communicates with the auricle which empties into the muscular-walled ventricle. By contraction of the ventricle, blood is forced into the ventral aorta, valves preventing its return to the auricle. The ventral aorta runs forward and gives off paired afferent branchials which pass to the gill arches where they form capillaries. From the capillaries, the

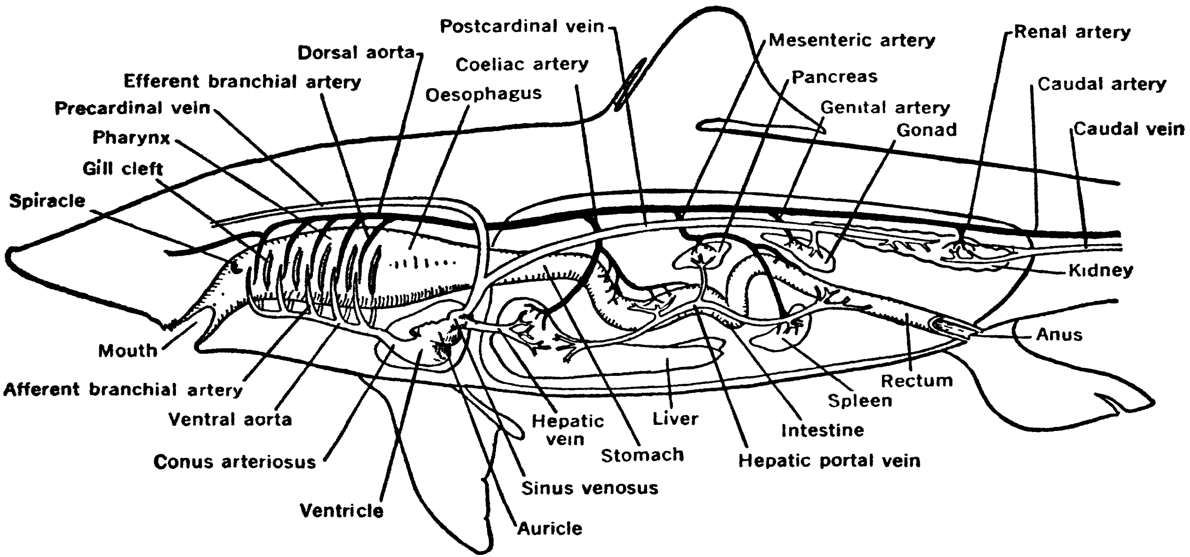


Fig. 307. Diagrammatic side view of the circulatory system of a dogfish. The arteries are in solid black, the veins in outline. (From Mavor, *General Biology*, by permission of The Macmillan Company, publishers.)

oxygenated blood is carried by efferent branchials to the single dorsal aorta. Anteriorly the dorsal aorta continues into the head region as the internal carotid, and posteriorly it passes just below the notochord, giving off branches which lead to capillaries in the other organs of this region. A subintestinal vein leads from the intestine to the hepatic portal system in the liver, and from the liver blood is returned by the hepatic vein, which empties into the sinus venosus. From the other organs anterior and posterior cardinals return the blood to the ducts of Cuvier, which empty into the sinus venosus. A single duct of Cuvier, the right, remains in the adult of this class.

FISHES. The heart of the fishes is two-chambered, as was that of the cyclostomes. The ventricle leads anteriorly into a muscular conus arteriosus, which continues as the non-muscular bulbus arteriosus, and then as the ventral aorta. The branchial vessels are less numerous than in the preceding class, but are essentially similar in other respects (Fig. 307). There are typically six pairs of afferent branchials in the embryos of all vertebrates. These are subject to much modification in the adult. In the fishes, as in all other vertebrates, the first arch disappears (Fig. 308 A), with the exception of that part which remains as the carotid artery supplying the head. The proximal portion of the second arch is also lost, while the distal portion forms a part of the carotids. The remaining pairs are retained in the fishes generally and, with the development of the gills and their capillaries, are divided into afferent and efferent branchials. The efferent branchials unite to form the dorsal aorta.

The dorsal aorta almost immediately gives off paired subclavians to the pectoral fins, and, more posteriorly, genitals to the gonads; coeliac and mesenterics to the intestine; renals to the kidneys; and pelvics to the pelvic fin. It then continues into the tail as the caudal artery. Blood is returned from the tail by the caudal vein, which splits near the cloaca, forming the renal portals, which lead to the capillary networks in the kidneys. From here renals lead to the postcardinals, which also receive blood from the reproductive organs and dorsal

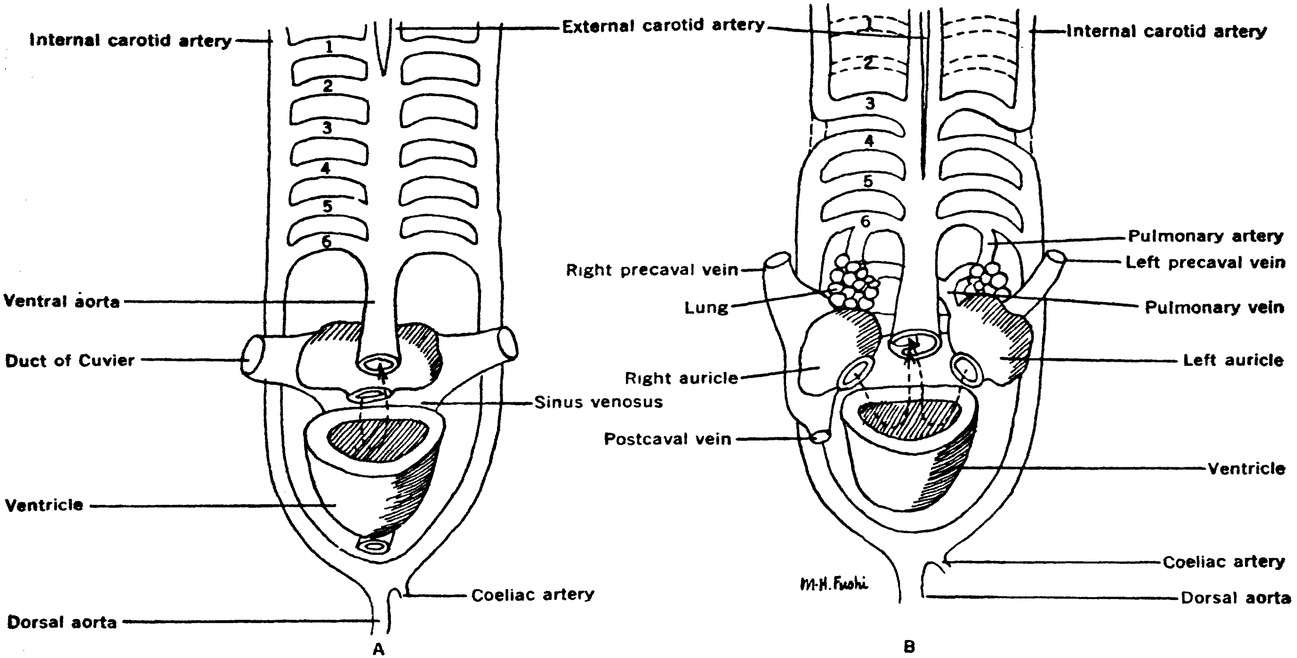


Fig. 308. Diagrams showing the heart and aortic arches. A, fishes; B, amphibians. The heart is represented as cut across, so that the observer is looking from the ventral side back into the ventricle, and forwards into the auricles and bases of the truncus and arterial arches. The numbers 1–6 represent the Aortic Arches. (Redrawn from De Beer, *Vertebrate Zoology*, by permission of The Macmillan Company, publishers.)

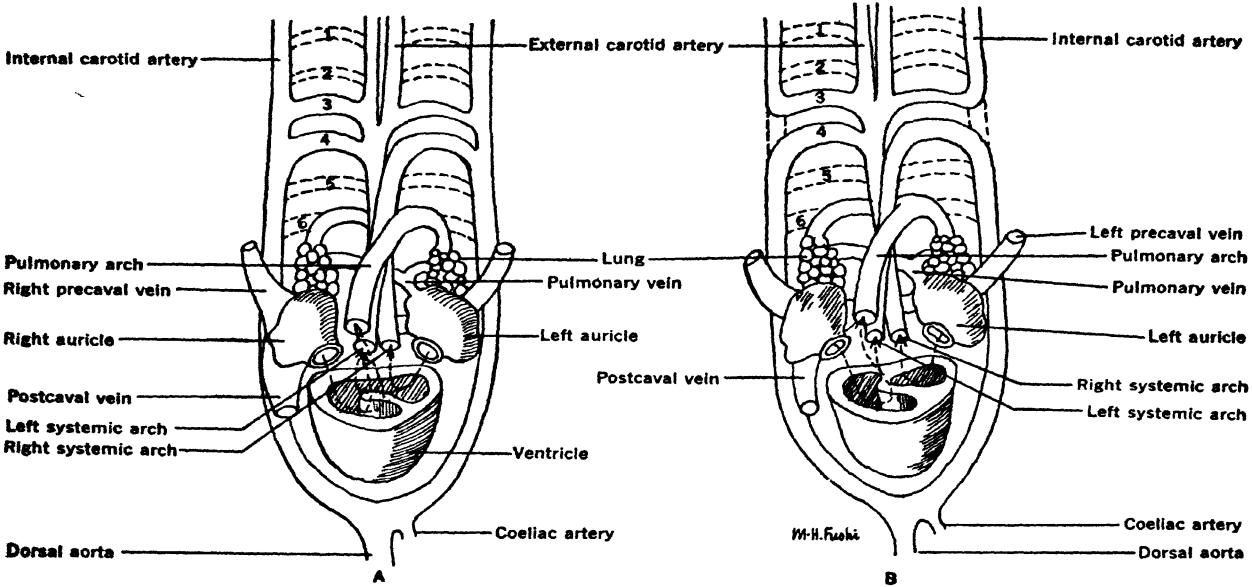


Fig. 309. Diagrams showing the heart and aortic arches. A, lizards; B, crocodiles. The heart is represented as cut across, so that the observer is looking from the ventral side back into the ventricle, and forwards into the auricles and bases of the truncus and arterial arches. The numbers 1–6 represent the Aortic Arches. (Redrawn from De Beer, *Vertebrate Zoology*, by permission of The Macmillan Company, publishers.)

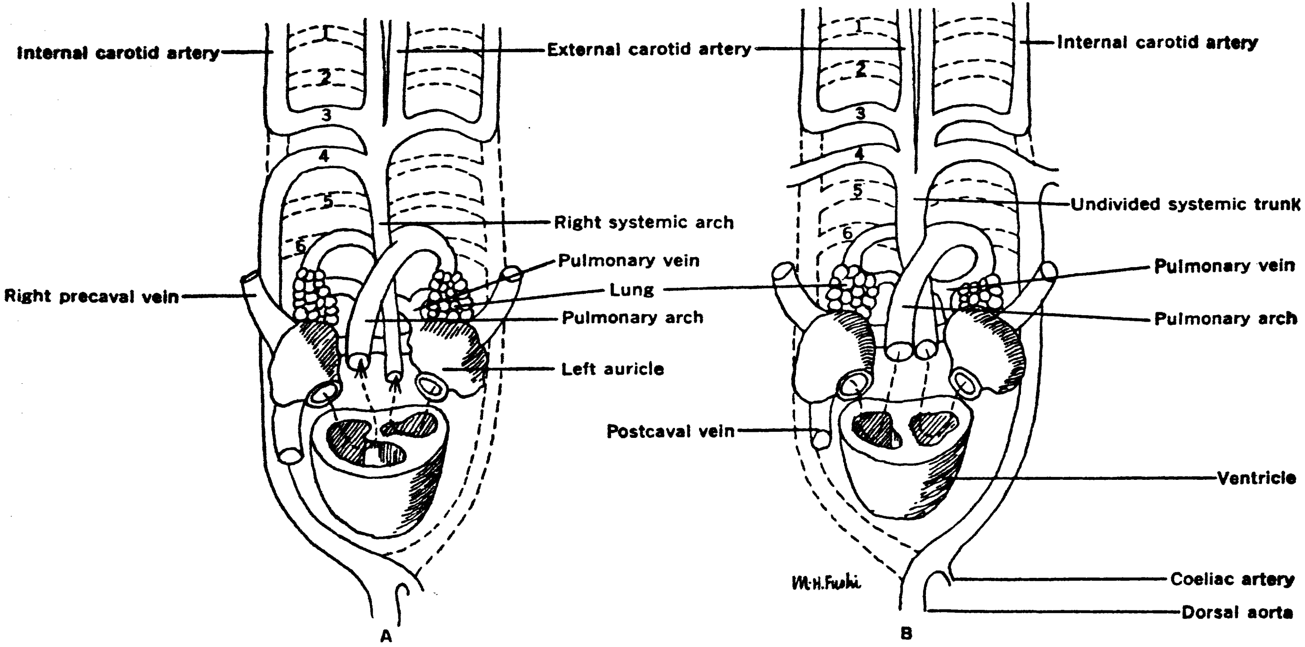


Fig. 310. Diagrams showing the heart and aortic arches. A, birds; B, mammals. The heart is represented as cut across, so that the observer is looking from the ventral side back into the ventricles, and forwards into the auricles and bases of the arterial arches. The numbers 1–6 represent the Aortic Arches. (Redrawn from De Beer, *Vertebrate Zoology*, by permission of The Macmillan Company, publishers.)

body wall before emptying into the sinus venosus. Paired lateral veins drain the ventral body wall and receive iliac and subclavian veins from the pelvic and pectoral fins, respectively, before emptying into the ducts of Cuvier. From the anterior part of the body blood is returned by way of the anterior cardinals and the inferior jugulars, both of which empty into the ducts of Cuvier.

A number of veins drain the alimentary canal and unite to form the hepatic portal, which is essentially the same as in the cyclostomes. Interesting variations are seen in those fishes in which the air bladder is used as a lung. In the Australian lungfish, pulmonary arteries arising from the posterior pair of efferent branchials lead to the walls of the air bladder. From the capillaries in the walls of the bladder, a pulmonary vein returns the blood to the left side of the auricle. An indication of the condition which is to follow in the amphibian is seen in the partial division of the auricle by a longitudinal septum.

AMPHIBIANS. In the larval amphibian, the circulatory system is essentially the same as that of the fishes (Fig. 311). In the adult, with the substitution of pulmocutaneous for branchial respiration, important changes are noted.

The heart is now a three-chambered organ, as the auricle is divided into two cavities by a complete septum. The pulmonary veins empty into the left auricle. The other veins lead into the sinus venosus which empties into the right auricle. A series of valves within the chambers and within the bulbus serve to partially separate arterial from venous blood.

In the anurans, the third branchial arches no longer continue dorsally to connect with the dorsal aortae, but remain with portions of the first and second to form the carotids. The fourth pair becomes the functional arches, the systemic trunks, which carry blood from the ventral to the dorsal aorta. The fifth disappears in this order, as in all higher vertebrates, while the proximal portion of the sixth arch remains on both sides, and from it the pulmonary arteries supply the lungs. The dorsal portions of the sixth remain for a time, connecting the pulmonaries with the dorsal aorta. These are known as the ducts of Botallus, and they eventually close, forming ligaments.

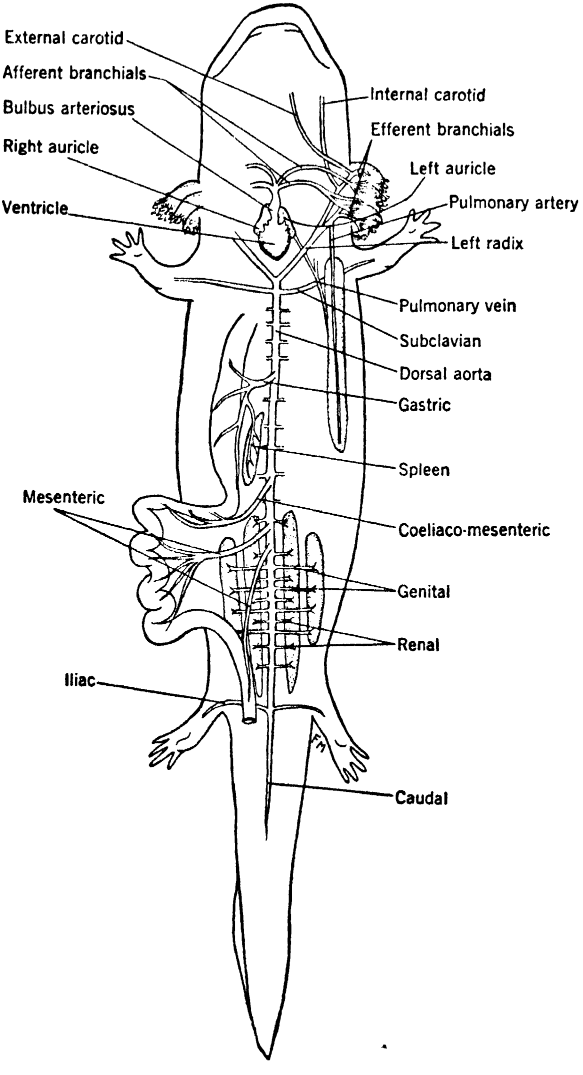


Fig. 311. The larger arteries of *Necturus*. (Adapted from Turtox Wall Chart, courtesy The General Biological Supply House, Chicago.)

The dorsal aorta gives off the usual branches supplying the various organs in different regions of the body. From the alimentary canal blood is returned through the hepatic portal system, as in the fishes. The renal portal system is also essentially similar to that previously described. A new vein, the postcava (inferior vena cava), is present, extending from the renals between the kidneys, through the liver, to the sinus venosus. The postcava receives the hepatic veins from the liver as it passes through that organ. It forms one of the main routes bringing blood from the posterior part of the body, and, in higher forms, very largely replaces the postcardinals.

Blood returning from the hind legs may pass through the iliacs directly into the renal portals, or it may pass through other vessels, the pelvics, which arise from the iliacs. The pelvics pass ventrally and unite to form the ventral abdominal, which courses anteriorly to the liver, where it communicates with parts of the hepatic portal system.

REPTILES. With the exception of the Crocodilia, the heart of reptiles consists of three chambers, two auricles and one ventricle. The ventricle opens into three large vessels (Fig. 313), the two systemic arches (fourth of the fishes) and the pulmonary, which soon branches into a right and a left vessel leading to the lungs. Pulmonary veins empty into the left auricle. As there is no connection between the pulmonary arteries and the dorsal aorta in the adult, the pulmonary circulation is now distinct.

The right systemic arch leads from the left side of the ventricle; the left aortic arch, from the opposite side. Because of this arrangement and the presence of an incomplete septum dividing the ventricle, the arterial blood brought to the left side of the ventricle by pulmonaries leaves by way of the right systemic arch. The left systemic arch contains mixed blood. The carotid arteries arise from the base of the right systemic and carry pure blood to the head.

In the order Crocodilia, the longitudinal septum in the ventricle is complete, forming a four-chambered heart very similar to that characteristic of birds and mammals. This results in a complete separation of arterial and venous blood within the heart. The systemic arches of the reptiles unite to form the dorsal aorta, the branches of which are very similar to those of the amphibians. With regard to the veins,

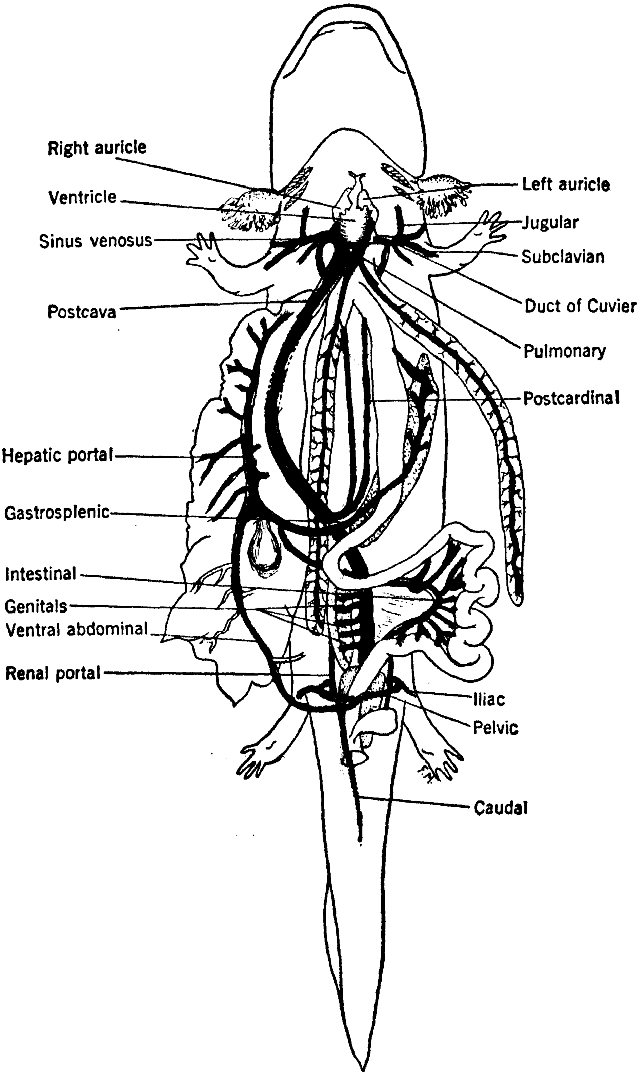


Fig. 312. The larger veins of *Necturus.* (Adapted from Turtox Wall Chart, courtesy The General Biological Supply House, Chicago.)

however, a number of changes are noted. The posterior cardinals are much reduced, the left disappearing entirely; the remainder of the right is now called the azygos vein. The renal portal system also is poorly developed as a result of the rise of a new type of kidney in the adult.

BIRDS. The avian circulatory system shows a considerable advance over that characteristic of the reptiles (Fig. 315).

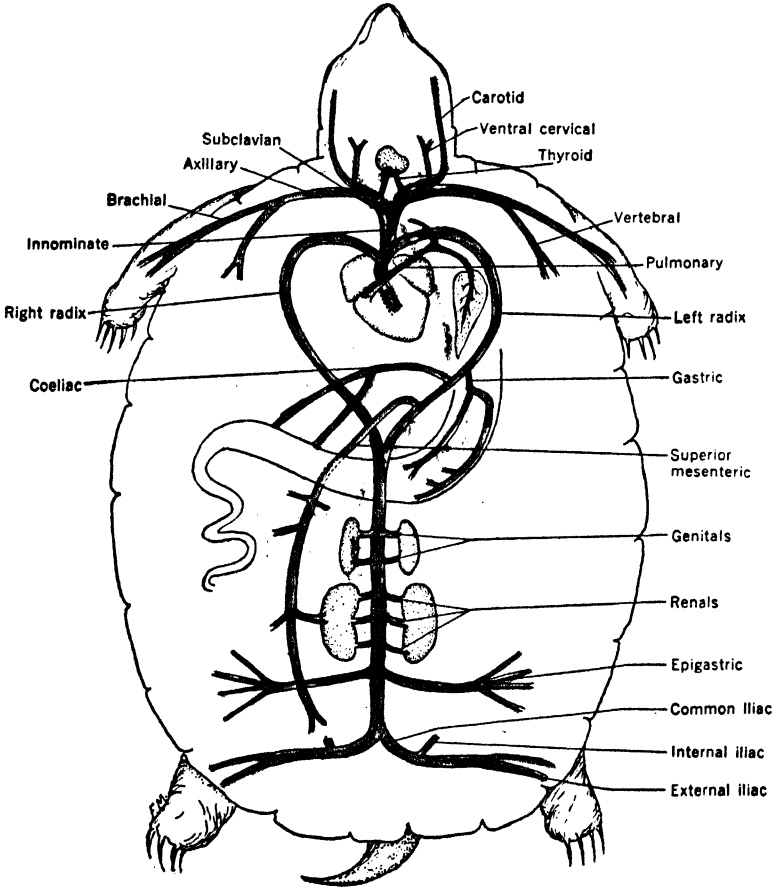


Fig. 313. The larger arteries of the turtle.

The heart is four-chambered. The left systemic arch has disappeared, and the right remains as the functional aorta leading from the left ventricle.

The right systemic arch gives off anteriorly a pair of large vessels, the innominate arteries. These later branch, giving rise to the common carotids and the subclavians. The arch then continues posteriorly as the dorsal aorta, giving rise to the usual arteries supplying the organs of the abdominal region and the hind limbs.

The pulmonary artery leads from the right ventricle to the lungs, while the pulmonary veins return blood to the left auricle. There is no sinus venosus; all venous blood is brought directly into the right auricle by the anterior (superior) and posterior (inferior) venae cavae (Fig. 316). The former of these is made up of the jugulars from the head and the subclavians from the fore legs.

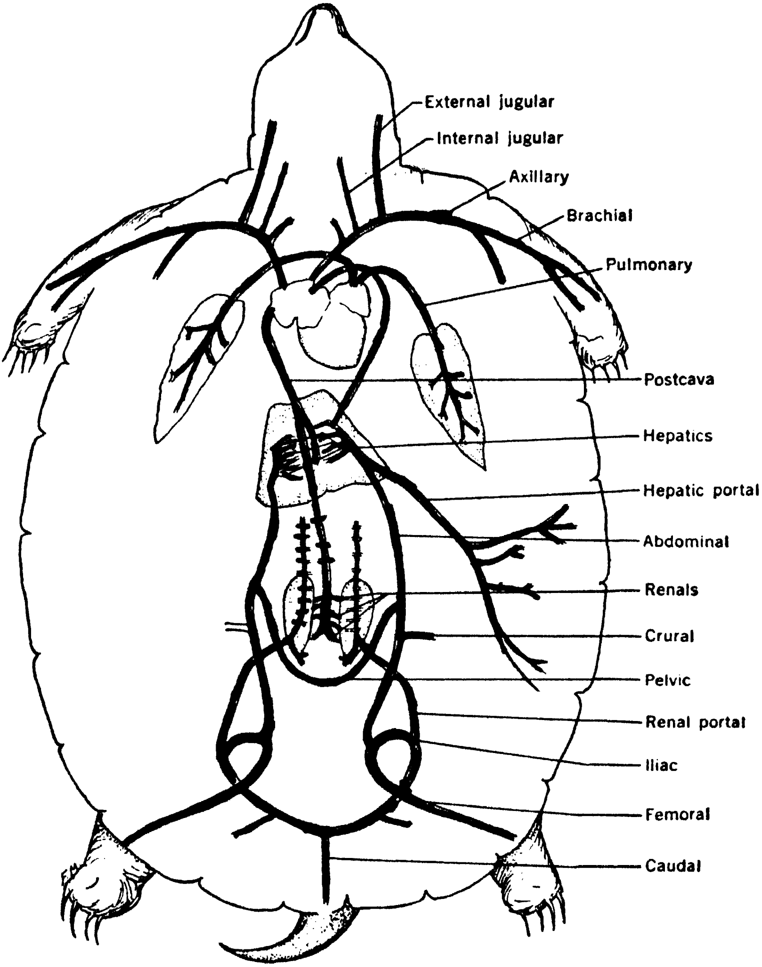


Fig. 314. The larger veins of the turtle.

The inferior vena cava is formed by the junction of the iliac veins. The latter are made up of femorals from the legs and renals from the kidneys. The caudal vein divides into renal portals, as described in the preceding classes. These connect directly with the iliac veins and also send branches into a system of capillaries in the kidneys.

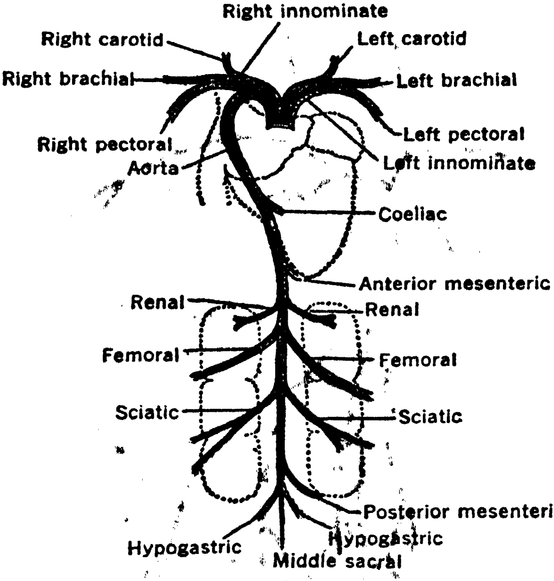


Fig. 315. Diagram of the principal arteries of a bird. (From Hegner, *College Zoölogy*, after Bradley, by permission of The Macmillan Company, publishers.)

MAMMALS. With a few exceptions, the plan of the circulatory system in mammals is surprisingly like that of the birds. One of the first noticeable differences is that the left systemic arch persists (Fig. 317), while the right largely disappears. The arch then gives off branches to the head and fore limb, and continues posteriorly as the dorsal aorta, giving off the customary branches to the viscera before dividing to form the common iliacs.

The main parts of the venous system are also similar to the condition seen in the birds, although there is much variation in details among the different mammals. The anterior venae cavae receive blood from the jugulars and subclavians (Fig.

318). In most forms, the left vessel joins with the right just anterior to the heart, thus forming a single precava.

The remains of the right posterior cardinal are represented by the azygos on the right side and the hemiazygos on the left. The latter connects with the azygos, which empties into the right superior vena cava. The inferior vena cava receives iliac and femoral veins from the legs, genitals from the gonads, renals from the kidneys, and hepatics from the liver, before emptying into the right auricle. The hepatic portal system is well developed, while the renal portal system has entirely disappeared.

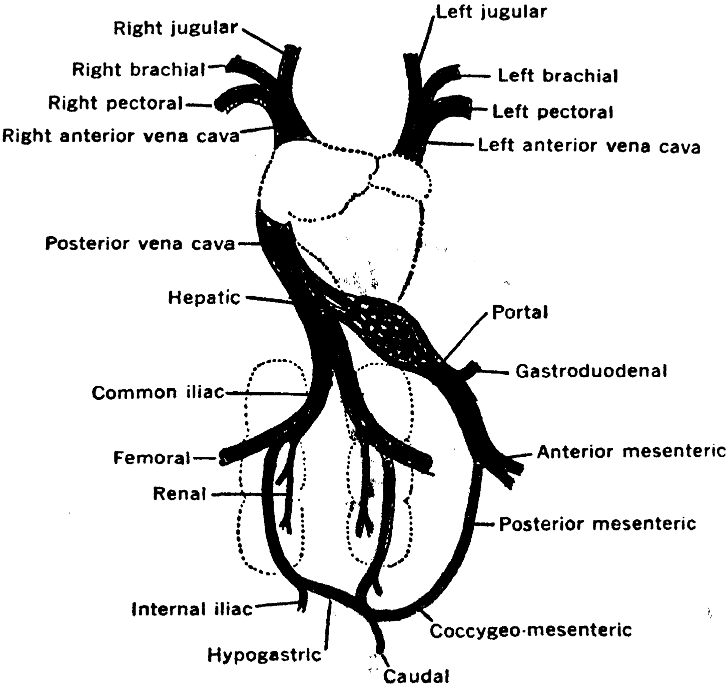


Fig. 316. Diagram of the principal veins of a bird. (From Hegner, *College Zoölogy*, after Bradley, by permission of The Macmillan Company, publishers.)

THE LYMPHATICS

As stated above, the lymphatics constitute a less definite series of spaces and vessels through which the lymph is circulated. Bear in mind that the direction of the flow of lymph is always toward the heart. This movement is very largely due to muscular movements of various parts of the body, but in some forms so-called lymph hearts are present.

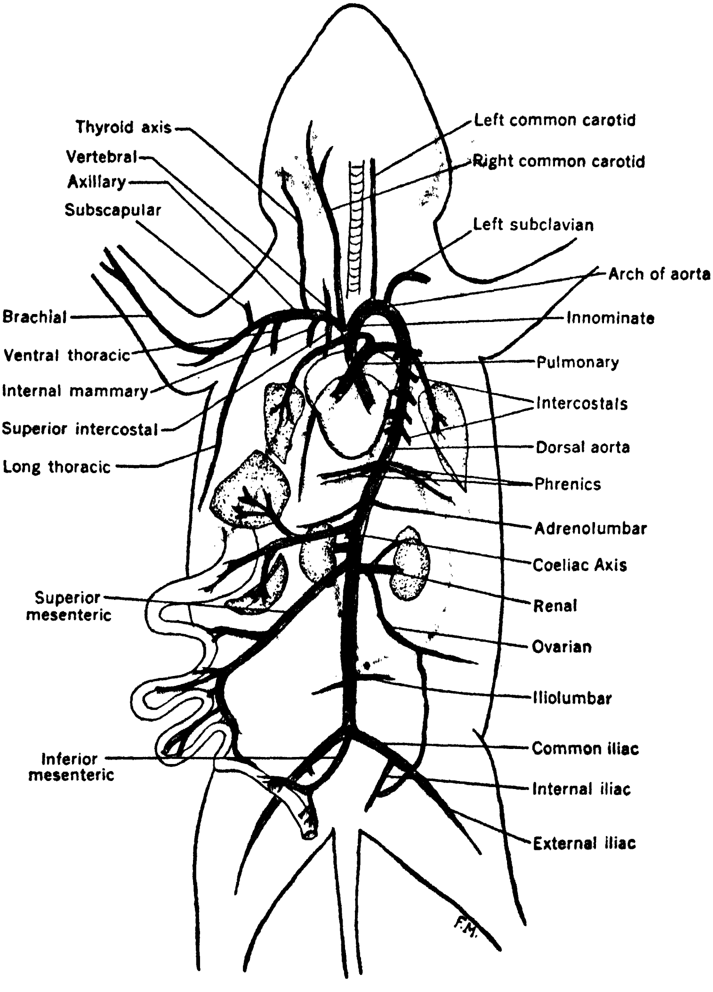


Fig. 317. The larger arteries of the white rat.

Because of the character of the vessels, it is difficult to trace a connected story of the phylogeny of the lymphatics. It is known that the lymphatic circulation is extensive in the fishes, particularly in their larval stages. In many forms there is a large lymph sac in the head region in which the bones of the skull are formed. There are also many species having large lymph spaces beneath the skin. In the eels there is a large amount of lymphoid tissue, and a lymph heart is present in the tail. This heart aids in returning lymph to the blood stream through a connection with the caudal vein. The subvertebral space opens into the venous system near the heart.

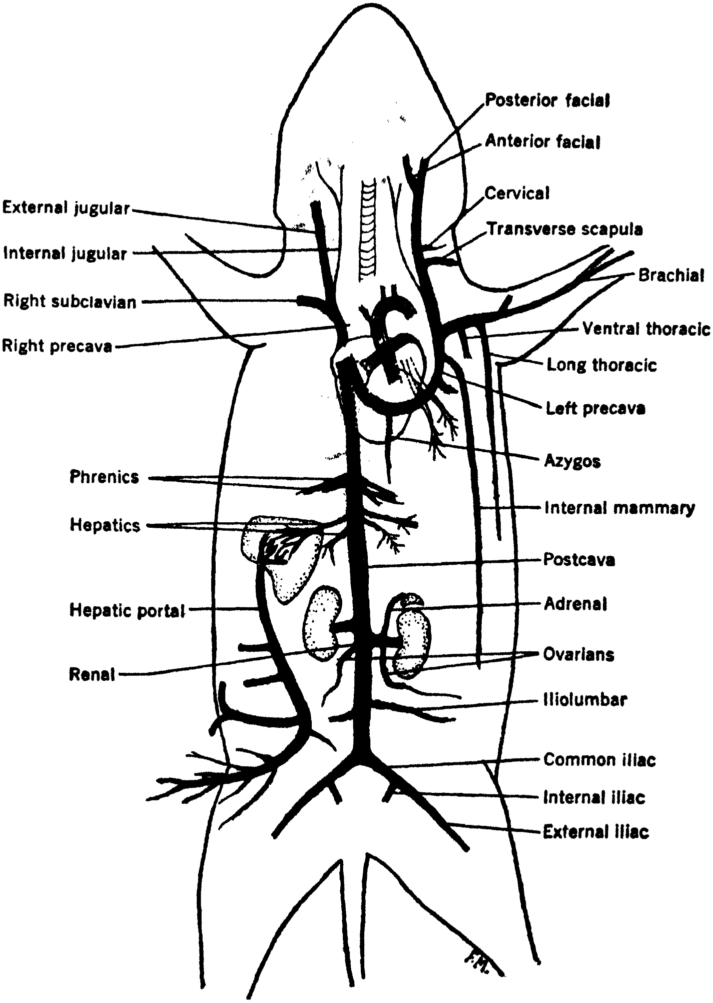


Fig. 318. The larger veins of the white rat.

In the amphibians the muscular-walled, pulsating lymph hearts are well developed. In the Gymnophiona there is a pair of such structures for each segment of the body. In the Caudata there are several pairs of lymph hearts along the posterior part of the lateral line. In the frog there are no well-developed lymphatic vessels, but the lymph flows within numerous large and irregular lymph spaces. Of these the subcutaneous sinuses are especially well developed. From these spaces lymph eventually reaches the four lymph hearts, located in relation to the four limbs. The anterior pair empties into the vertebral veins, which unite with the

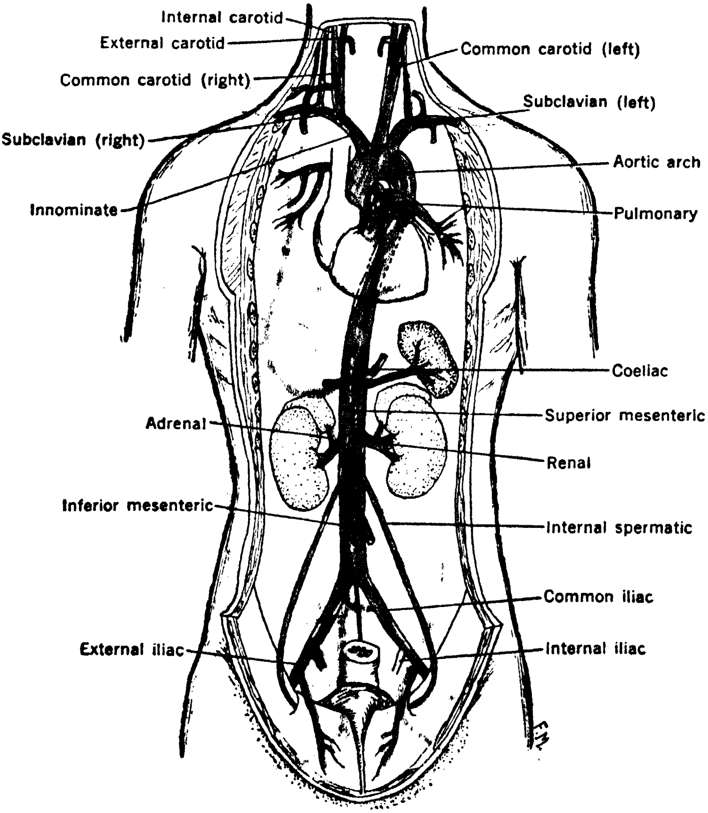


Fig. 319. The larger arteries of man. (Adapted from the American-Frohse Anatomical Charts, courtesy of A. J. Nystrom and Company, Chicago.)

internal jugulars. The posterior hearts lie opposite the end of the urostyle and empty into the transverse iliac veins. The return of the lymph to the hearts is prevented by semilunar valves at their openings into the veins.

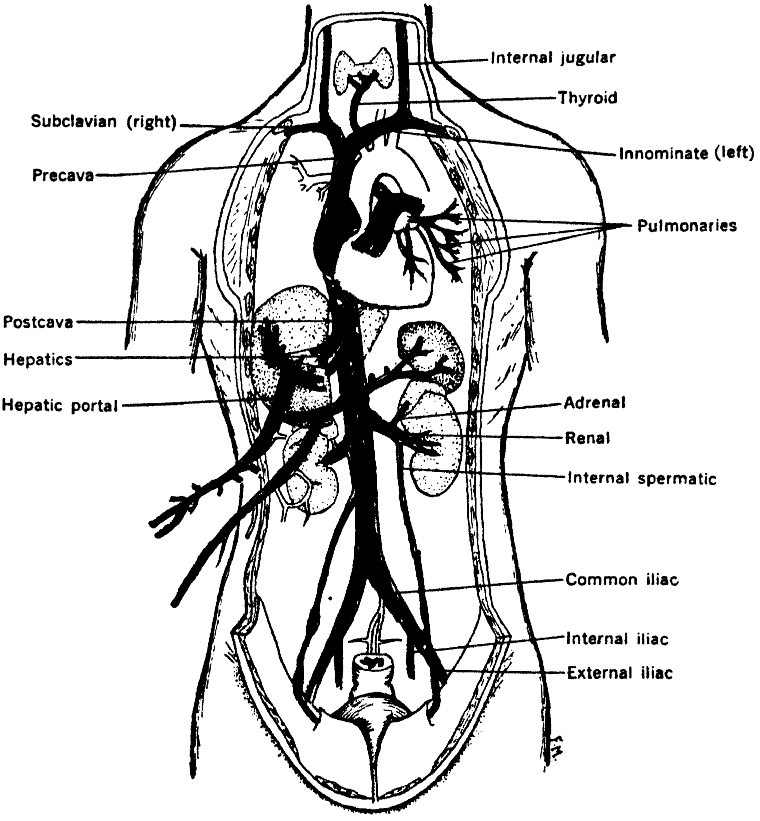


Fig. 320. The larger veins of man. (Adapted from the American-Frohse Anatomical Charts, courtesy of A. J. Nystrom and Company, Chicago.)

In reptiles the anterior lymph hearts disappear. A pair of definite vessels, the thoracic ducts, lie along the sides of the vertebral column and empty into the anterior venae cavae near the heart.

In the birds no lymph hearts remain. The thoracic ducts are present as the most definite parts of the system, and are similar to those of the reptiles in their location and relation to the blood vessels.

The adult mammals also are without lymph hearts. The thoracic ducts are paired in the embryo, but typically only the left remains. This empties into the venous system near the junction of the left subclavian and the left external jugular veins.

In man the thoracic duct is a large vessel draining the legs, the abdomen, and a greater part of the thorax. It receives the left jugular from the head and the left subclavian from the left arm, and empties into the blood stream at the junction of the left jugular and the left subclavian veins. The right side of the head is drained by the right jugular, and the right arm by the right subclavian. These unite to form the right lymphatic duct, which empties into the venous system between the right jugular and the right subclavian veins.

Lymph nodes and the larger lymph glands, such as the spleen and thymus, which have previously been referred to, are especially extensive in the mammals.

FUNCTIONS OF THE CIRCULATORY SYSTEM

From the preceding description, it will be seen that the circulatory system has numerous functions, among which the following may be mentioned:

1. The distribution of food material by leucocytes and lymph from the digestive tract to the tissue cells.
2. Distribution of oxygen by the erythrocytes from the respiratory membranes to the tissue cells.
3. Transportation by the lymph and blood of waste products of metabolism from the cells to the organs of excretion.
4. The distribution of chemical substances (hormones) from the ductless glands to all parts of the body.
5. The equalization of body temperature, resulting from oxidation of the tissues.
6. Defense against harmful organisms, by the phagocytic action of leucocytes, and by the formation within the blood stream of such chemical substances as antibodies.

SUMMARY

The circulatory system is concerned with the distribution of various materials throughout the body. It consists of blood and lymph and the various tubular vessels through which they flow. Blood is a fluid, consisting of the liquid plasma and cellular components, the red and white corpuscles. The red corpuscles are the carriers of oxygen, while the white ones aid in the removal of broken-down tissues and in the destruction of harmful bodies. The blood vessels include the heart, arteries, veins, and capillaries. These form a closed system of connecting tubules reaching all parts of the body. Lymph is a thin, watery fluid resembling blood except for the absence of the red cells. It occupies the spaces between the various cells of the body. The lymph vessels begin in these indefinite spaces which lead into ducts which in turn eventually empty into some vein.

In an early stage of development in vertebrates generally the circulatory system consists of a complete circuit of vessels from the yolk sac through the embryo and back to the yolk sac. With the development of additional organs in the body of the embryo, arteries supplying them branch off from the vessels first formed. In a similar manner veins develop which carry the blood from these organs to the heart. With the development of the alimentary canal important vessels arise which eventually take the place of those coming from the yolk sac. Associated with the developing liver and kidneys is the development of the hepatic portal and renal portal systems. The latter is reduced in birds and is not present at all in mammals.

In the gill-breathing vertebrates a series of aortic arches pass through the gill septa between the dorsal and the ventral aortae. Branches from these pass through the respiratory membranes of the gills. In terrestrial vertebrates these arches are present in the embryo only. The more anterior ones take part in the formation of the carotid arteries supplying the head, while portions of the last arch give rise to the pulmonary arteries leading to the lungs.

The lymphatic vessels are much less definite than are the blood vessels. Large lymph spaces or sinuses are present in the fishes and the amphibians. In the amphibians four small lymph hearts are present. These aid in returning the lymph to the venous system. Two such hearts remain in the reptiles but the birds and mammals are without them.

The most important lymph vessel in the mammals is the thoracic duct which drains a greater part of the posterior region of the body. Many lymph nodes and larger lymph glands are present in mammals.

XII. The Excretory System

The necessity for the removal of the waste products of metabolism has been pointed out in preceding chapters. The role of the circulatory system in transporting these wastes to their place of removal has also been referred to in the chapter on circulation. The organs which remove these various materials from the blood stream and convey them out of the body form the excretory system.

THE ORGANS OF EXCRETION

The principal materials eliminated from the body by the excretory organs are carbon dioxide, water, and solutions of various solids, particularly nitrogen-containing substances. A large proportion of the carbon dioxide resulting from oxidation within the tissues is eliminated from the blood stream through the respiratory membranes. The function of the skin, gills, and lungs as excretory organs was treated in connection with their role in respiration. The skin of mammals also is an important organ of excretion through the activity of the sweat glands, which were described with the other derivatives of the integument. A large amount of water and a small proportion of nitrogenous waste are eliminated through the activities of these glands, particularly in hot weather.

In spite of the importance of the excretory activities of the sweat glands and of the respiratory organs, the kidneys are usually thought of as the chief organs of excretion in the vertebrates. In discussing the structure of the excretory system, therefore, we are concerned with the kidneys, their ducts, and the urinary bladder. Although the liver is, as we have seen, mainly a digestive gland, it is also concerned with excretion through the part it plays in the formation of urea, one of the main constituents of urine, the excretion of the kidney. The kidneys and their ducts, particularly in the lower vertebrates, are so closely related to the reproductive ducts that the two systems are often studied together in the laboratory as the urogenital system.

The Excretory Unit

The fundamental unit of the excretory system is a small coiled tube, the uriniferous tubule. Such tubules are essentially similar in structure but not in their origin to the nephridia, the excretory tubules characteristic of the nonchordates (Fig. 321). It should be recalled that these nephridia, in a form like the earthworm, are paired, segmentally arranged tubules with one end, the nephrostome, in communication with the body cavity, and with the other, the nephridiopore, opening to the exterior through the body wall. The waste materials are obtained directly from the body fluids and discharged to the outside through the nephridiopore.

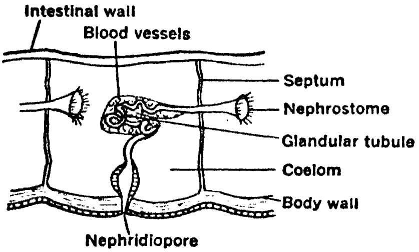


Fig. 321. Diagram of a protonephridium of an annelid worm. (Redrawn from Walter, *Biology of the Vertebrates*, after Galloway, by permission of The Macmillan Company, publishers.)

A number of important differences from this plan are seen in the vertebrates. In the first place, the tubules of the adult are typically grouped together to form definite organs, the kidneys, and their excretions are poured into a common duct which drains the entire organ. Secondly, the former communication with the coelomic cavity is lost (except in the lower forms), the wastes being brought to the tubules by the blood stream.

The typical vertebrate kidney consists of a large number of these coiled tubules (Fig. 322), which empty into a common duct. The end of each tubule is indented, forming a cup-shaped, expanded portion known as Bowman's capsule. A glomerulus, consisting of a knot of capillaries, projects into each capsule. The glomerulus is formed between an artery branching from the dorsal aorta and a vein leading to the postcardinal in some vertebrates and to the postcava in others. Bowman's capsule and the glomerulus together form a body known as the Malpighian corpuscle. Beyond the Malpighian body the tubule is convoluted for a short distance and is known as the proximal convoluted tubule. Following this, the tubule straightens out and later makes a hairpin turn which is known as Henle's loop. This consists of descending and ascending limbs. A second convoluted tubule (the distal) follows; after which the entire tubule empties into a collecting tubule. The collecting tubules receive the excretions from numerous uriniferous tubules and then empty into the pelvis, a cavity within the kidney. The pelvis is the expanded portion of the ureter, the excretory duct which conducts the urine away from the kidney. The excretory ducts empty into the cloaca in some vertebrates, while in others they lead to a temporary storage place, the urinary bladder.

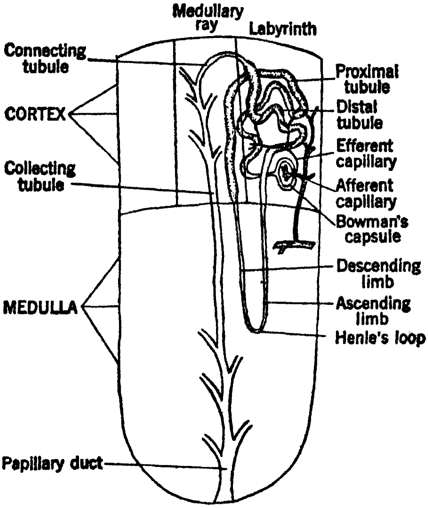


Fig. 322. Diagram of a urinary unit. (Redrawn from Walter, *Biology of the Vertebrates*, after Piersol, by permission of The Macmillan Company, publishers.)

EMBRYOLOGY

During its development, the excretory system of the higher vertebrates passes through two important stages, both of which remain as the permanent system of lower groups. The first of these, the pronephric type, appears in the embryo of all vertebrates. It is the functional system in the larval stages of many fishes and amphibians, and in some of the cyclostomes (Myxinoidea) persists in the adult as the functional organ (Fig. 323). In all other vertebrates the pronephric tubules are replaced by those of the mesonephric type, which are the functional organs of most fishes and amphibians. In reptiles, birds, and mammals this system functions only in the embryo, being in turn replaced by a third type, the metanephric.

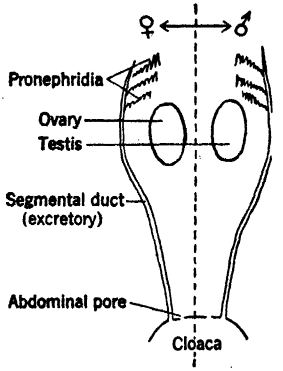


Fig. 323. Pronephridial stage of certain cyclostomes. Female represented on the left; male on the right. (Redrawn from Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

The kidney of these three systems is known as the pronephros, mesonephros, and metanephros, respectively. In each case the organ consists of a series of tubules of mesodermal origin, being derived from that central portion of the mesodermal somites previously referred to as the mesomere (Fig. 124). That portion of the mesomere which gives rise to the tubules is known as the nephrotome (Fig. 325). The cavities within the segmentally arranged nephrotomes are the nephrocoels. These open into the body cavity by ciliated funnels, the nephrostomes. From the nephrostomes, the Bowman's capsules are formed and these surround the glomeruli, which are formed between small arteries from the dorsal aorta and veins which lead into the postcardinal. From each Bowman's capsule a tube develops which grows posteriorly to unite with the tubules of the succeeding segments. In this manner, a collecting duct is formed. Tubules of this character obviously receive excretory products from two sources, from the coelom through the nephrostomes and from the blood stream by way of the glomeruli.

In the vertebrates generally, the pronephros consists of a few paired tubules in the anterior part of the abdominal cavity. In the human embryo there are seven pairs of tubules formed, beginning at the seventh segment. The more anterior of these begin to degenerate before the posterior ones develop. The free end of the collecting duct, which grows caudally to empty into the cloaca, is known as the pronephric duct.

In the pronephric system there are no capsules developed immediately surrounding the glomeruli. The nephrostomes and glomeruli are merely closely related, lying opposite one another across a narrow portion of the coelom.

As development continues, the pronephros disappears, but the greater part of the pronephric duct remains as the excretory duct of the succeeding system, the mesonephric. The meso-

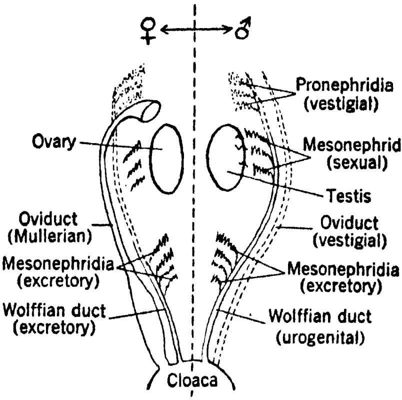


Fig. 324. Mesonephridial stage of the amphibians. Female represented on the left; male on the right. (Redrawn from Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

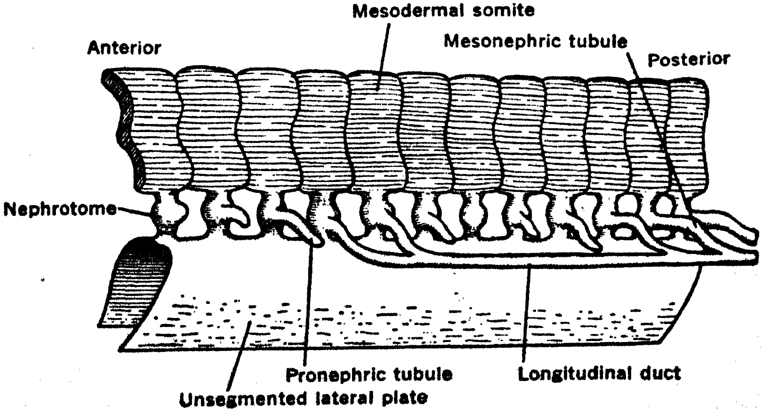


Fig. 325. Diagram showing development of pronephric and mesonephric tubules from nephrotomes. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

nephros consists also of a series of paired tubules similar to those of the pronephros, but taking their origin in more posterior segments (Fig. 324). Each mesonephridium definitely surrounds a glomerulus to form a Bowman's capsule. The mesonephros develops no new duct but utilizes the pronephric duct, the tubules emptying into it posterior to the position of the pronephros. That portion of the pronephric duct anterior to the connection with the mesonephridia disintegrates. The remaining portion, which drains the mesonephros, is now known as the mesonephric duct. The mesonephros is also known as the Wolffian body and its duct as the Wolffian duct.

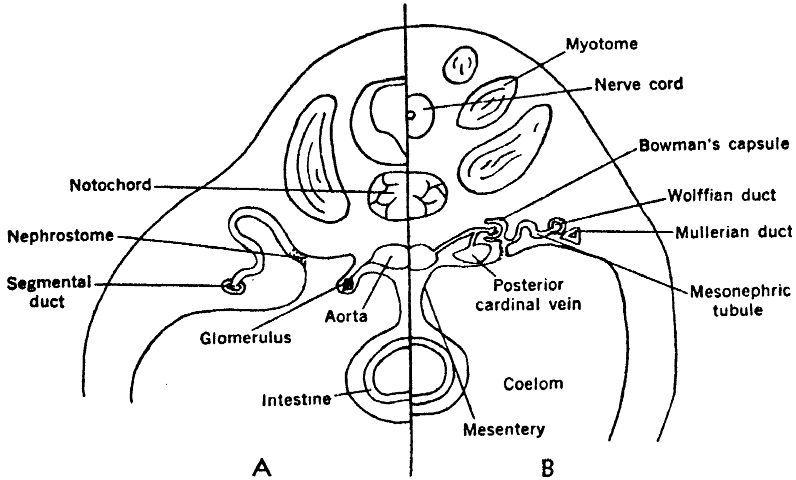


Fig. 326. Cross section diagrams showing two stages in the development of the nephridia. A, pronephric stage; B, mesonephric stage. (Redrawn from Walter, *Biology of the Vertebrates*, after Wiedersheim, by permission of The Macmillan Company, publishers.)

The mesonephros is a large body in all vertebrates and its tubules have lost their original segmental arrangement. It is the functional kidney of fishes and amphibians. In some groups the nephrostomes open into the coelom (Fig. 326), while in others this relationship has been lost.

In reptiles, birds, and mammals, the mesonephros is succeeded by the metanephros (Fig. 327), which is the functional adult kidney of these three classes. The tubules of the metanephros are similar in origin to those of the preceding system. They arise in segments posterior to those giving rise to the mesonephros. In no case is there a nephrostome present in this type of tubule. The Malpighian body is located at the end of the tubule rather than on a side branch, as is the case when nephrostomes are present. A new excretory duct, the ureter, appears as an evagination from the posterior part of the mesonephric duct. This tube extends anteriorly and eventually establishes connections with the metanephric tubules.

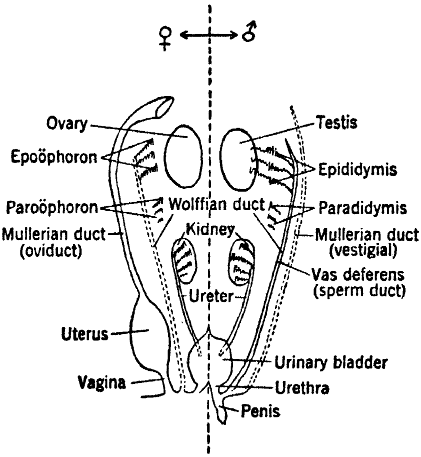


Fig. 327. Metanephridial stage of reptiles, birds, and mammals. Female represented on the left; male on the right. (Redrawn from Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

Portions of the mesonephric system are retained in these higher vertebrate classes, where they are associated with the function of reproduction. They will be discussed in the description of the reproductive system in the following chapter.

COMPARATIVE ANATOMY

Cyclostomes. In this group, the excretory system consists of a pair of long and narrow kidneys extending through a greater part of the length of the body cavity. These are drained by ducts which unite in the region of the anus, forming a sinus which opens to the outside through a pore just posterior to the anus. In *Petromyzon* the functional kidney is a mesonephros, although the pronephros may remain throughout life. In some myxinoids both pronephros and mesonephros are retained, and it is thought that in these forms the pronephros may be functional throughout life.

Fishes. The mesonephric system is characteristic of fishes, although parts of the pronephros seem to persist in certain teleosts.

In the Elasmobranchii (Fig. 328), Chondrostei, and Holostei, the nephrostomes remain open, particularly those at the anterior end of the organ.

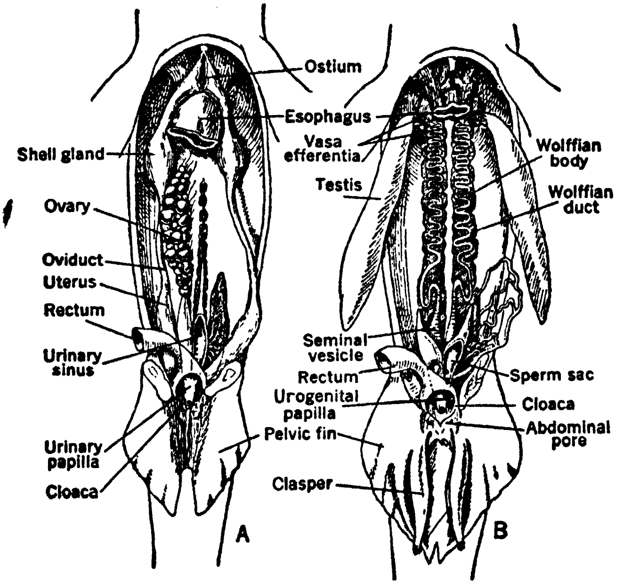


Fig. 328. Diagrams of the urogenital organs of an elasmobranch, *Scyllium canicula.* A, female; B, male. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Bourne, by permission of The Macmillan Company, publishers.)

The kidneys are narrow, elongated bodies lying outside the peritoneum, just ventral to the vertebral column. There is much variation in the ducts, especially in their relation to the reproductive system, in the various groups of fishes.

In the male elasmobranch, the tubules of the anterior part of the kidney are connected with the tubules of the testis and are used by the sperm cells in passing from the testis to the mesonephric duct, which is, thus, a urogenital duct. The anterior part of the kidney in such cases is largely given over to a reproductive function, and is, therefore, often referred to as the sexual mesonephros. The posterior part of the kidney retains its excretory function. Its tubules are drained by the accessory mesonephric duct. The accessory (excretory) and the mesonephric ducts of the two sides unite, forming a urogenital sinus. This is a cavity within a urogenital papilla which opens into the cloaca through a single urogenital pore.

In the female elasmobranch the kidney is not associated with the reproductive glands. The mesonephric ducts are entirely urinary in function, and unite to form a urinary sinus within a urinary papilla, from which the urinary pore opens into the cloaca. At either side of the papilla are the separate openings of the reproductive ducts (oviducts) which lead from the coelom rather than directly from the ovaries.

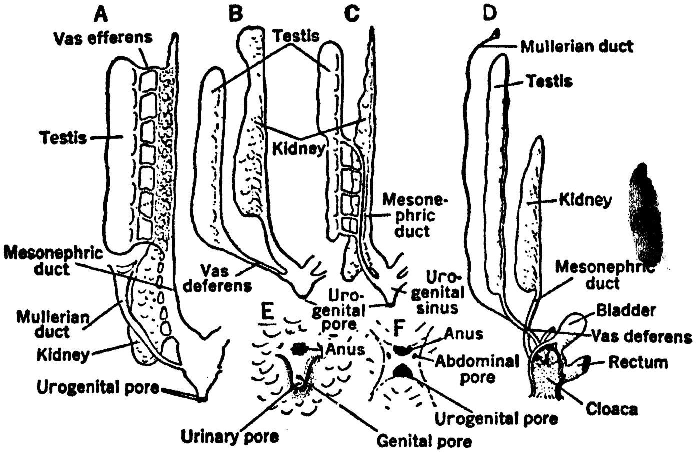


Fig. 329. Diagrams of the urogenital system of male fishes. A, *Acipenser;* B, a teleost; C, *Polypterus;* D, *Protopterus;* E, cloaca of female *Salmo;* F, cloaca of male *Polypterus.* (From Goodrich, *Studies on the Structure and Development of Vertebrates.* C, after Budgett; D, after Parker; F, after Budgett. By permission of The Macmillan Company, publishers.)

In the teleostomous fishes generally there is no connection between the excretory and reproductive systems (Fig. 329). The mesonephric kidney is entirely excretory in both sexes. Fusion of the two kidneys occurs frequently in this group. The ducts unite to form a urinary sinus which opens to the exterior by a single urinary aperture. The reproductive ducts in both sexes also unite and open to the exterior by means of a single genital opening. The excretory and reproductive ducts may unite before reaching the external surface; in such cases a single opening, the urogenital pore, is present.

A urinary bladder is present in most teleostomous fishes, although apparently not serving as a place for the storage of urine as is the case in mammals. This structure in this group is formed as an enlargement of the excretory duct. Each duct may give rise to a separate bladder, or the enlargement may take place posterior to the union of the two ducts, forming thereby a single bladder. In the Dipnoi the urinary bladder resembles that of the amphibian in being formed by the evagination of the wall of the cloaca.

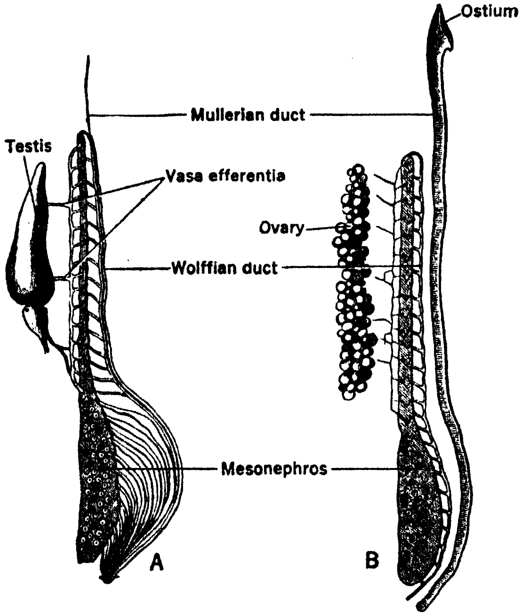


Fig. 330. Diagrams of the urogenital system of a urodele, *Triton.* A, male; B, female. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Spengel, by permission of The Macmillan Company, publishers.)

AMPHIBIANS. The excretory system of the amphibian is also of the mesonephric type. In many species the nephrostomes remain permanently open. The shape of the kidney is dependent upon that of the body as a whole. In the Gymnophiona and Caudata (Fig. 330), these structures are elongated bodies, narrow at the anterior end but widening posteriorly. In the short-bodied frogs and toads they are much more compact and are confined to the posterior part of the body cavity.

In the male, as in the elasmobranchs, the tubules of the anterior portion of the kidney have a reproductive function. Sperm cells pass through them from the testis to the Wolffian duct, which functions, therefore, as a sperm duct, or vas deferens. The more posterior tubules are entirely excretory in function and drain into the posterior part of the Wolffian duct. These urogenital ducts empty separately into the cloaca.

In the female the kidneys are entirely excretory in function, and the Wolffian ducts are excretory ducts which empty separately into the cloaca.

The urinary bladder is an evagination of the ventral wall of the cloaca, and is of somewhat doubtful function, although the presence of urea in its contents has been demonstrated in the frog.

REPTILES. The functional excretory organ of the adult, in all animals above the class Amphibia, is of the metanephric type (Fig. 331). This type of kidney is concerned with excretion only. Portions of the mesonephros which remain make up parts of the reproductive system, especially in the male. As would be expected from the origin of the ducts of the metanephric system, a close relation between the posterior parts of the excretory and reproductive systems persists. This relationship is subject to much variation in details within the class.

The shape of the kidneys is subject to considerable variation in the different reptiles. In the lizards and crocodiles the kidneys are elongate bodies located in the posterior part of the body cavity. In the snakes they are long and slender bodies, lying one behind the other, rather than on opposite sides of the body cavity. The more compact kidney characteristic of the turtles illustrates an evolutionary tendency which is further carried out in the birds and mammals. As in teleosts, fusion of the posterior ends of the kidneys is not uncommon in the lizards.

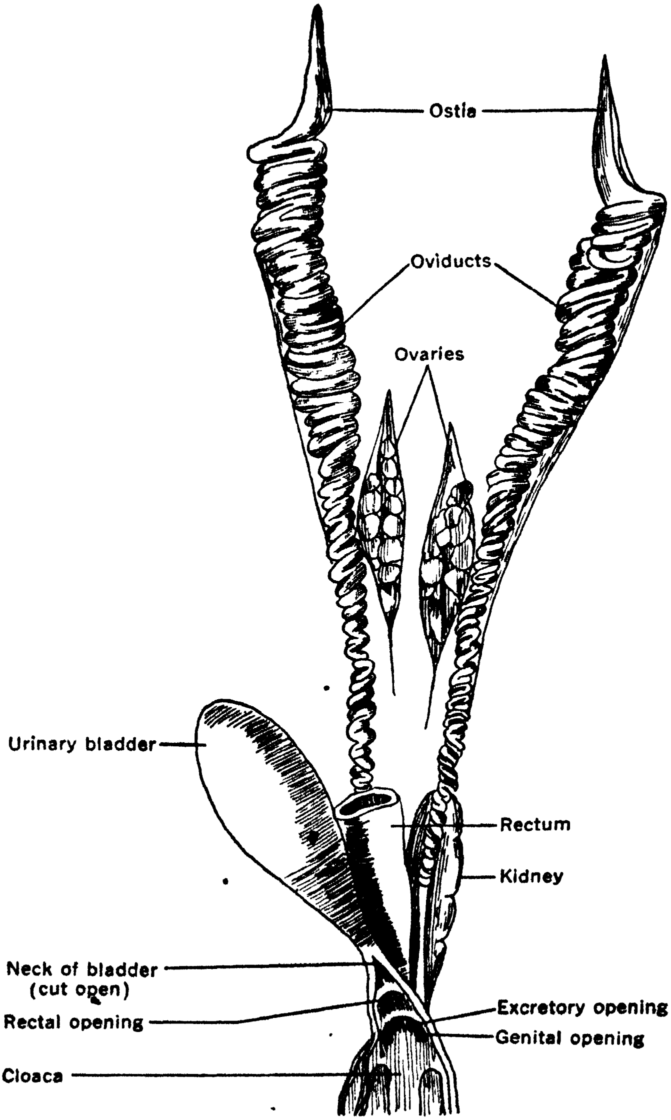


Fig. 331. Female urogenital organs of a lizard, *Lacerta muralis.* (Redrawn from Wiedersheim, *Comparative Anatomy of Vertebrates*, by permission of The Macmillan Company, publishers.)

The excretory ducts, which are now known as ureters, empty directly into the cloaca in a majority of reptiles. When a bladder is present, as in the turtles and some lizards, the ureters discharge the excretions into this organ, which in turn communicates with the cloaca.

The reptilian bladder is considered by most embryologists to be an allantoic bladder, that is, formed by an enlargement of the posterior part of the allantoic stalk remaining within the body. Such a structure is present in turtles (Fig. 332) and in some lizards, while in other reptiles the entire allantois apparently degenerates.

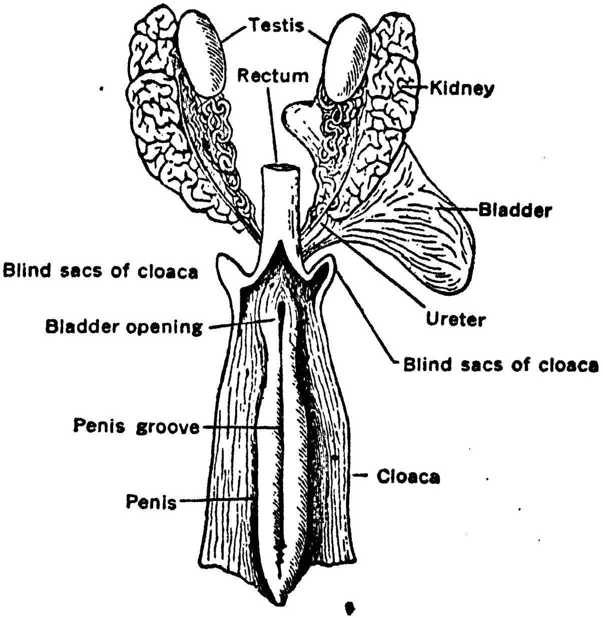


Fig. 332. Cloaca and urogenital organs of a male turtle, *Chelydra serpentina.* (From Hegner, *College Zoölogy*, after Gegenbaur, by permission of The Macmillan Company, publishers.)

Birds. In the birds (Fig. 333), the kidneys are compact lobate bodies tucked away in concave spaces within the pelvic girdle. As in some other forms previously referred to, the two kidneys frequently unite. The urinary unit is essentially the same as in the other classes which have a metanephric excretory organ. The renal portal system is reduced as

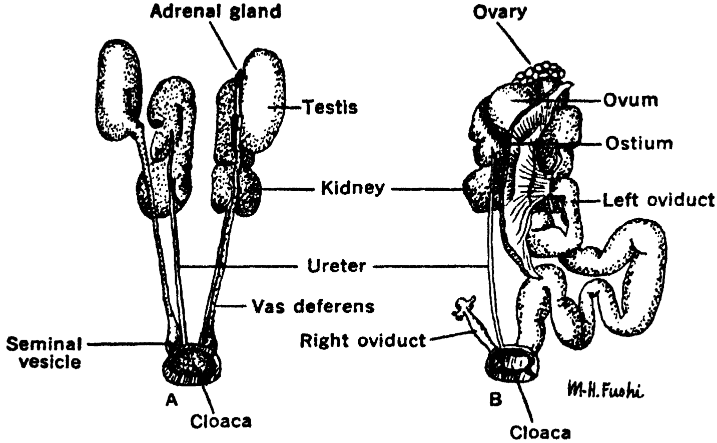


Fig. 333. Diagrams of the urogenital organs of a bird, *Columba livia.* A, male; B, female. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Parker, by permission of The Macmillan Company, publishers.)

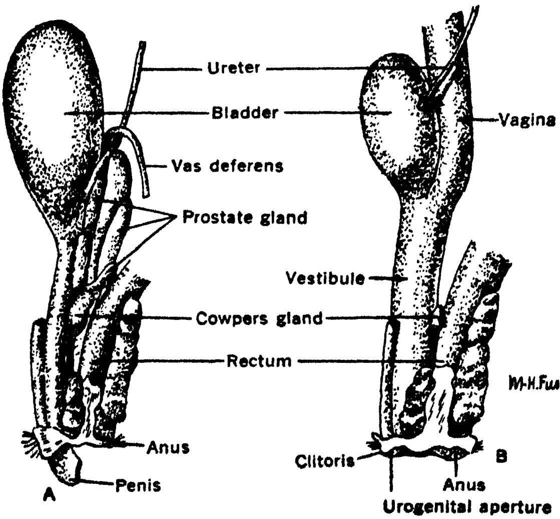


Fig. 334. The urogenital organs of a mammal, *Lepus caniculus.* A, male; B, female. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Parker, by permission of The Macmillan Company, publishers.)

compared with its development in the reptiles. Renal portal veins are present. These empty into the iliac veins after sending branches into the kidneys. The kidneys receive arterial blood from the dorsal aorta through the renal arteries, and they are drained by renal veins which empty into the inferior vena cava.

The ureters are short ducts which empty into the cloaca, there being no urinary bladder present.

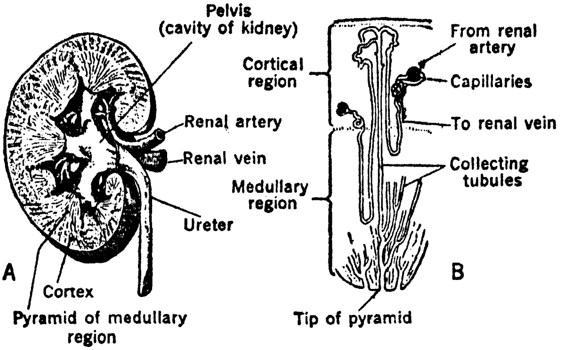


Fig. 335. Excretory organs of man. A, longitudinal section of a kidney; B, urinary tubules. (From Hegner, *College Zoölogy*, after Peabody and Hunt, by permission of The Macmillan Company, publishers.)

MAMMALS. The mammalian kidney differs from that of the preceding classes in being a more compact organ. Although divided into many lobes in the embryo the kidney of most mammals changes to the bean-shaped organ characteristic of the class. The kidney of the human embryo, for example, is lobed, but this condition disappears shortly after birth. Such mammals as the bear (Fig. 336) and cow, as well as many of the water-living types, retain the lobate character of these organs.

The kidneys of mammals lie in the dorsal part of the body cavity, and in some forms are loosely suspended within it, although surrounded by a peritoneal covering outside of which they originate. While in most lower forms these organs are symmetrically placed side by side, in mammals one kidney is frequently anterior to the other. In man, for example, the left kidney is usually anterior to the right, while in the cat the reverse is true.

The typical mammalian kidney as seen externally is a bean-shaped organ with a convex lateral and a concave medial margin. The depression on the inner margin is known as the hilus. Here the renal artery and renal nerves enter the kidney, while the renal vein and the ureter pass out.

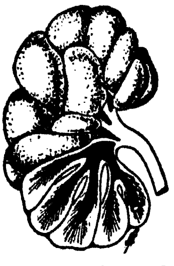


Fig. 336. Left lobulated kidney of a bear, partly dissected. (From Walter, *Biology of the Vertebrates*, after Henle, by permission of The Macmillan Company, publishers.)

Internally (Fig. 335), the substance of the kidney consists of two differentiated regions, an outer cortex and an inner medulla. The latter is further subdivided into a number of cone-shaped segments, the pyramids, the apices of which project into a cavity, the pelvis. The pelvis is the funnel-shaped expanded portion of the ureter within the kidney. The mass of Malpighian corpuscles, together with a large part of the tubules, is located in the cortical part of the kidney. Within the medulla are the blood vessels going to and from the glomeruli and the larger collecting tubules emptying into the pelvis.

The ureters carry the excretory wastes away from the kidney and empty into the urinary bladder. In most mammals the ureters enter the bladder by an oblique passage through its walls. The urinary bladder is of the allantoic type. Its highly muscular walls are capable of wide distention. Draining the bladder is a single duct, the urethra. In the male the reproductive ducts unite with the urethra slightly posterior to the bladder. Distally, therefore, the urethra becomes a urogenital sinus which leads to the external urogenital opening. In the female, the urethra is an excretory duct with an external opening close to, but in most instances distinct from, that of the reproductive duct.

SUMMARY

The excretory system is concerned with the removal of the waste products of metabolism. The chief waste materials are carbon dioxide, water, and nitrogen-containing substances. The respiratory organs play an important part in the elimination of carbon dioxide and water. In the mammals the sweat glands also aid in excretion. Morphologically, however, it is customary to consider the excretory system as including the kidneys, the excretory ducts, and the urinary bladder.

The functional unit of the kidney is the uriniferous tubule. This is, essentially, a coiled tubule, with one end (closed) in close relation to a blood vessel, and the other end leading to the excretory duct. In the lower vertebrates the tubules also open into the coelomic cavity, but in the higher forms this opening is not present.

The excretory ducts drain the kidneys and lead directly to the external opening in some forms, in others to a temporary storage place, the urinary bladder. The excretory duct is often closely related to the reproductive duct, particularly in the male.

Three successive types of kidneys are seen in the development of the excretory system of a higher vertebrate. These are the pronephros, the mesonephros, and the metanephros. With a very few exceptions the pronephros is a nonfunctional and merely embryonic type of kidney. The mesonephros is the functional kidney in fishes and amphibians; the metanephros in reptiles, birds, and mammals. Portions of the mesonephric kidney remain in these higher classes, where they are associated with the reproductive system.

There is much variation as to detail in the various parts of the excretory system in the different vertebrate classes. In cyclostomes and fishes generally the ducts unite to form a sinus before the external surface is reached. In teleostomous fishes a tubular bladder is formed as an expansion of the duct. In the male elasmobranchs the tubules of the anterior part of the mesonephros are connected with reproductive tubules from the testis. In the female elasmobranch and in both sexes of teleostomous fishes the tubules of the kidney are not associated with the reproductive system.

The excretory system of the amphibians is very similar to that of the fishes. The kidney is of the mesonephric type, and in the male, the anterior portion is concerned with reproduction. The bladder is an evagination of the ventral wall of the cloaca.

In the reptiles the kidney is a metanephros and is concerned with excretion only. Portions of the mesonephros remain and are associated with the reproductive system, particularly in the male. The excretory ducts, ureters, empty directly into the cloaca in many species. Turtles and some lizards possess a urinary bladder.

The avian kidney is also a metanephros. The ureters empty into the cloaca, there being no urinary bladder.

The kidney of most mammals (metanephros) is a bean-shaped organ, with the concave margin directed medially. As seen in section it is composed of an inner medulla and an outer cortex. The ureters empty into a urinary bladder which is drained by the urethra. In male mammals the reproductive ducts empty into the urethra, which then becomes a urogenital duct.

XIII. The Reproductive System

The various systems previously described are concerned, as we have seen, with the welfare of the individual animal. The reproductive system to which we now turn our attention provides for the perpetuation of the species of which the individual is a representative.

PARTS OF THE SYSTEM

The reproductive system of the vertebrates consists of the following kinds of structures: the germ cells, the union of which begins the development of a new organism; the gonads, those organs in which the germ cells undergo their development; various types of structures taking part in bringing the germ cells together, thereby insuring fertilization; and, finally, those organs in which the fertilized egg undergoes development.

The germ cells, the female egg and the male sperm, are the essential reproductive units, all other structures associated with this function being concerned in one way or another with their welfare. These germ cells have been referred to by Weismann and others as constituting an "immortal germ plasm." It is important to understand the distinction between this so-called germ plasm which lives on from one generation to the next, and the somatoplasm, including all the other tissues of the body, which perishes with the individual. Of the various parts of the reproductive system, the germ cells alone consist of germ plasm. All other parts of the system consist of somatoplasm, that is, of muscle, epithelium, and connective and other tissues which have often been referred to in the preceding pages.

THE GERM CELLS. The structure and development of the typical vertebrate germ cells have been described in Chapter V. The facts presented there should be reviewed at this time.

THE GONADS. The organs in which the germ cells undergo development are typically paired bodies of mesodermal origin located in the dorsal part of the body cavity at either side of the mesentery proper. They are of two kinds, the ovaries in the female and the testes in the male. The former are usually suspended in the body cavity by a mesentery, the mesovarium; the latter, by a similar peritoneal fold, the mesorchium. With a few exceptions the sexes are separate in the vertebrates, testes and ovaries developing in different individuals. The hagfish, *Myxine*, apparently produces sperms at certain times and eggs at others.

Although typically present in pairs, single gonads are characteristic of several vertebrates. In *Petromyzon* and the perch, the two ovaries unite, while in several other species only one ovary develops. In the birds (Fig. 333 B), while both are present in embryonic life, only one ovary, the left, develops into a functional organ.

STRUCTURES INSURING FERTILIZATION. Among the structures which aid in bringing about the union of the germ cells may be mentioned the ducts which carry them to the place of fertilization; the various copulatory organs used, by those forms in which fertilization is internal, to introduce the sperms into the oviduct of the female; and numerous glands which produce a wide variety of secretions.

Among the vertebrates in general, those forms in which internal fertilization is the rule produce relatively few eggs. Where fertilization takes place externally, as in most fishes and amphibians, a large number of eggs are matured and liberated periodically. In the latter case it is obvious that the chance that an egg will meet a sperm is much less than when internal fertilization is practised. The large number of eggs produced increases the probability that some of them will be fertilized.

ORGANS FOR THE CARE OF THE FERTILIZED EGG. A large number of structures are developed in the different vertebrate classes for the protection of the egg itself or of the developing embryo. In oviparous animals having internal fertilization, glands are present which add a protective covering, or shell, to the egg after it has been fertilized. In viviparous animals a portion of the oviduct is expanded, forming a structure known as the uterus, in which the fertilized egg passes through various stages of development.

In exceptional cases among lower vertebrates (oviparous forms) provision is made for the care of the fertilized egg after leaving the oviduct of the female. Certain teleosts, such as the sea horse (*Hippocampus*) and allied forms, possess a pouch, or sac, on the ventral surface of the body of the male. The eggs are deposited in these sacs. In some amphibians eggs are carried in pits or pockets in the skin, and in one genus (*Rhinoderma*) the vocal sacs are temporarily employed for the same purpose. The integumentary pouch of the marsupials and monotremes among the mammals serves a similar function in providing protection for the immaturely born young in one case and a brood sac for the fertilized egg in the other.

In all true terrestrial vertebrates, the embryonic membranes, the amnion and allantois, are structures coming under this classification. Finally, we should list here the placenta, a structure characteristic of all mammals above the marsupials. This consists of numerous villi, formed from the surface of the chorion, which dovetail between similar villi on the uterine wall. Both surfaces being richly supplied with capillaries, the placenta provides for the interchange of nutritive materials and waste products between the maternal and embryonic (allantoic) circulation (Fig. 344).

EMBRYOLOGY

As has been mentioned previously, the development of the reproductive organs is closely associated with that of the excretory system. The gonads first appear in the form of genital ridges (Fig. 337), located in the median dorsal part of the body cavity between the nephrostomes and the dorsal mesentery. As development continues, connective tissue, nerves, and blood vessels are added to these organs, which now bulge out into the coelom, where they lie suspended by mesenteries. The gonads are invaded by the potential germ cells.

In the male the interior of the developing gonad eventually becomes hollowed out to form a number of small tubules, in the walls of which the germ cells are developed into mature sperms. These seminiferous tubules lead out from the testis as the vasa efferentia, which establish communication with the excretory tubules of the anterior part of the mesonephros. The mature sperm cells, as should be recalled, pass through these tubules and leave the body by way of the Wolffian duct, which becomes, therefore, a sperm duct, the ductus (vas) deferens. In those vertebrates which retain the mesonephros as the functional kidney, the Wolffian duct is also an excretory duct. With the substitution of the metanephric kidney and the development of a new urinary duct, the ureter, in reptiles, birds, and mammals, the Wolffian duct functions as a sperm duct (vas deferens) only. In these forms the tubules of the anterior part of the mesonephros, which remain as functional connections between the vasa efferentia and the vas deferens, form what is called the epididymis. Vestiges of the tubules of the posterior portion of the mesonephros may remain, forming a small body called the paradidymis.

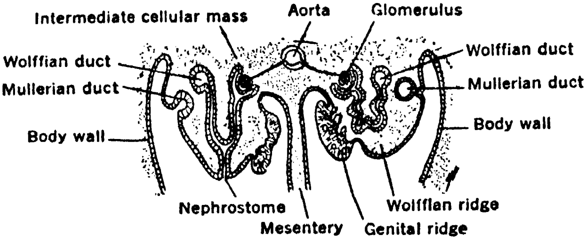


Fig. 337. Diagrammatic section across the Wolffian and genital ridges, to show the origin and relations of the Mullerian ducts and tubules of the Wolffian body. (From Walter, *Biology of the Vertebrates*, after Pasteau, by permission of The Macmillan Company, publishers.)

In the female, the gonad remains more or less solid internally, and the developing eggs move about within the organ until mature. In most vertebrates, with a few exceptions to be noted later, the ripened egg breaks through the wall of the ovary into the body cavity. It then finds its way into the ostium, the opening into the oviduct, through which it passes to the place of fertilization. This reproductive duct in the female is known as the Mullerian duct, and it has no functional relation to the excretory system. Its origin varies in different vertebrates. In the elasmobranch fishes it is formed by the longitudinal splitting of the Wolffian duct; in some cases it develops by the closing of a groove in the peritoneal lining of the cavity lateral to the Wolffian duct and in still others by the hollowing out of a solid column of cells arising in the same general location. It is believed by some that the ostium represents the nephrostome of one of the anterior nephridia.

Although the mesonephros is of no functional importance in the female of those forms which have a metanephros, it is of interest to note that portions of this organ remain. These vestigial bodies, known as the epoöphoron and the paroophoron, represent respectively remains of the anterior and posterior parts of the mesonephros.

That an oviduct also develops in the male is shown by the presence of a well-developed Mullerian duct in numerous instances in the adult, as in *Rana pipiens*, the leopard frog, and *Mustelus*, the smooth dogfish. Vestiges of this duct remain in higher forms, even in man, in the form of such structures as the appendix testis and the uterus masculinus.

The many specialized structures which develop subsequently in different parts of the system and which are characteristic of the different vertebrate classes will be considered below in a description of the comparative morphology of the system.

COMPARATIVE ANATOMY

Cyclostomes. In this group the gonads are elongated bodies suspended freely in the coelom. In *Petromyzon* a single gonad is present, apparently formed by the fusion of the originally paired bodies. The hagfish also has a single gonad in the adult because in development one of them degenerates. In both sexes the germ cells are discharged directly into the body cavity. Near the junction of the two excretory ducts are a pair of small openings which communicate with the coelom. Through these openings, the genital pores, the germ cells pass into the urogenital sinus and through it to the outside. In some forms, as in *Petromyzon*, the urogenital opening is at the end of a papilla located just posterior to the anus. The absence of genital ducts is a characteristic of the cyclostomes.

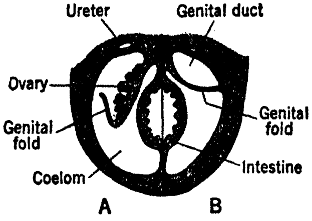


Fig. 338. Diagrammatic transverse sections of a teleost; on left through the ovary, on right more posteriorly through the genital duct. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

Fishes. There is so much variation in the organs of reproduction in the fishes that it is difficult to describe a typical condition.

In the elasmobranchs, as in lower vertebrates generally, the testes have a definite size and shape, while the ovaries are subject to much variation at different periods of the year, depending upon the condition of the eggs within. In both sexes the gonads are situated in the anterior portion of the body cavity (Fig. 328).

In the male, vasa efferentia convey the sperms to the tubules of the anterior part of the mesonephros (epididymis) which, in turn, lead into the Wolffian duct. The two Wolffian ducts unite posteriorly, forming a urogenital sinus which opens into the cloaca through the urogenital pore, located at the end of a urogenital papilla. Before uniting, each Wolffian duct enlarges to form the seminal vesicle. In those forms which practice internal fertilization, copulatory organs, the claspers, are developed from the medial margin of each pelvic fin. During copulation sperm cells are conveyed along grooves on the claspers into the cloaca and then into the oviducts of the female.

In the female the eggs break through the wall of the ovary into the body cavity and enter the oviducts through a single opening, the ostium, located ventral to the anterior part of the liver. A short distance from the ostium, each oviduct bears a shell gland, which secretes a covering around the egg as it passes through the duct. The posterior part of the oviduct in the viviparous species is expanded to form a large uterus, in which the fertilized egg is retained during its development. In other forms the fertilized eggs leave the body, and subsequent development takes place in the water, as in most true aquatic vertebrates. The oviducts open separately into the cloaca at either side of the median urinary papilla. Two abdominal pores open into the posterior part of the cloaca. These apparently have no reproductive function.

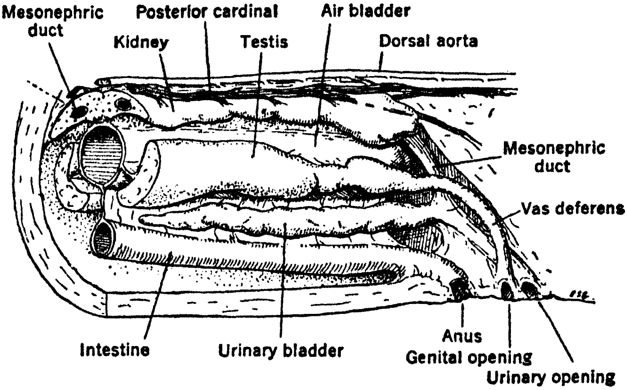


Fig. 339. Diagram of dissection of male fish, *Esox lucius*, showing relation of excretory and genital ducts. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

The reproductive system of the typical teleost fish is very different from that of other vertebrates in several respects (Fig. 339). The gonads frequently unite posteriorly and thus there is a single duct leading to the external opening. Even in the male the usual relation with the mesonephros is absent. In some cases there is a separate genital pore between the anus and the excretory opening. In other forms there is a common urogenital opening, the genital duct having united with the mesonephric duct. In the female the eggs do not enter the body cavity directly, but pass through canals which develop from the body cavity. In some forms the oviduct appears to be directly connected with the ovary, while in others a fold of peritoneum invests the ovary and the beginning of the oviduct, bringing them together (Fig. 338). As in the male, the genital and excretory ducts may or may not open separately. In either case no cloaca is present.

The reproductive system of the lungfishes is similar to that of the elasmobranchs. The usual relation with the mesonephros is characteristic of the male, while the eggs must pass through the body cavity in the female. The ducts empty into a cloaca, and abdominal pores are present.

AMPHIBIANS. In a typical amphibian the reproductive system is very similar to that of the elasmobranchs. In the male frog, for example, sperms pass from the testis through vasa efferentia to the tubules of the anterior part of the mesonephric kidney. These lead to the Wolffian duct, which is, in this case, a urogenital duct. Each duct opens separately into the cloaca, after widening out to form seminal vesicles.

In *Triton*, one of the newts, the excretory tubules do not connect with the Wolffian ducts until slightly before the latter reach the cloaca (Fig. 330). A greater part of the Wolffian duct is, therefore, in this case, a sperm duct.

In the female amphibian, the eggs are discharged into the body cavity. They enter the oviducts through their openings, the ostia. The oviducts of the frog are long and much-coiled tubes, each expanding posteriorly to form a uterus before emptying separately into the cloaca.

REPTILES. In the reptiles, as in all other amniotes, the mesonephros has been replaced as a functional kidney by the metanephros. In the male, however, the mesonephric duct remains and functions as the genital duct. The mesonephric tubules of the anterior end of the kidney remain as the epididymis and are connected with the tubules of the testis by the vasa efferentia. In the other direction the tubules of the epididymis lead into the mesonephric duct, which is the sperm duct, or vas deferens.

Several types of copulatory organs, or penes, are developed in the male reptiles. Snakes and lizards generally possess paired structures, the hemipenes. These are modifications of the cloacal wall, which may be everted and inserted into the cloaca of the female.

In the turtles (Fig. 348) and crocodiles a single penis is characteristic. This is a slightly erectile and protrusible grooved structure, through which the sperm cells may be carried into the cloaca of the female.

The reproductive system of the female reptile (Fig. 331) is not essentially different from that of the amphibian. The ovaries of crocodiles and turtles are typically solid organs, while those of snakes and lizards are hollow. In the latter type fertilization may take place within the ovary. In reptiles generally, the ova break through the wall of the ovary and reach the open ends of the oviducts after passing through the coelom. In snakes the right ovary is somewhat anterior to the left.

Internal fertilization is the characteristic method employed by the reptiles, and many of the snakes and lizards are viviparous. The reptilian egg is oval or elliptical in shape, and is covered by a tough membranous shell secreted by glands in the wall of the oviduct. In viviparous reptiles the posterior portion of the oviduct typically enlarges to form a uterus, in which the fertilized eggs undergo development.

The presence of an amnion and an allantois in this class of vertebrates, as previously described, has made possible development of an embryo independent of an aquatic habitat.

Birds. As would be expected from the close relationship of the two classes, the reproductive system of the birds is very similar to that of the reptiles. Fertilization is internal and the class is oviparous. In most birds there is no true copulation, the sperm being transmitted directly from the cloaca of the male to that of the female. In a few types such as the ostrich, penes resembling those of the crocodiles are present. The relatively large eggs are fertilized in the anterior portion of the oviduct and are covered with layers of albumen and finally by a shell, secreted by glands in the wall of the oviduct. Although both ovaries and both oviducts are present in early stages of development, those of the left side only persist as functional organs in the adult.

In the male both testes remain, and each is connected by a vas deferens to a seminal vesicle from which the sperms are discharged into the cloaca.

Mammals. Much variation, especially in details, is found in the reproductive system of the mammals. With the exception of the monotremes, the mammalian egg is relatively small and has little yolk. Fertilization is always internal, and, with the exception of monotremes, all members of the class are viviparous. As might be expected from this fact, the most distinctive features of the system in this group are those modifications associated with insuring fertilization of the eggs, which are produced in relatively small numbers, and with the subsequent care of the fertilized egg and the developing embryo. The relation between the parts of the reproductive and excretory systems is fundamentally the same as in the birds and reptiles, since the mammals also have a metanephric kidney.

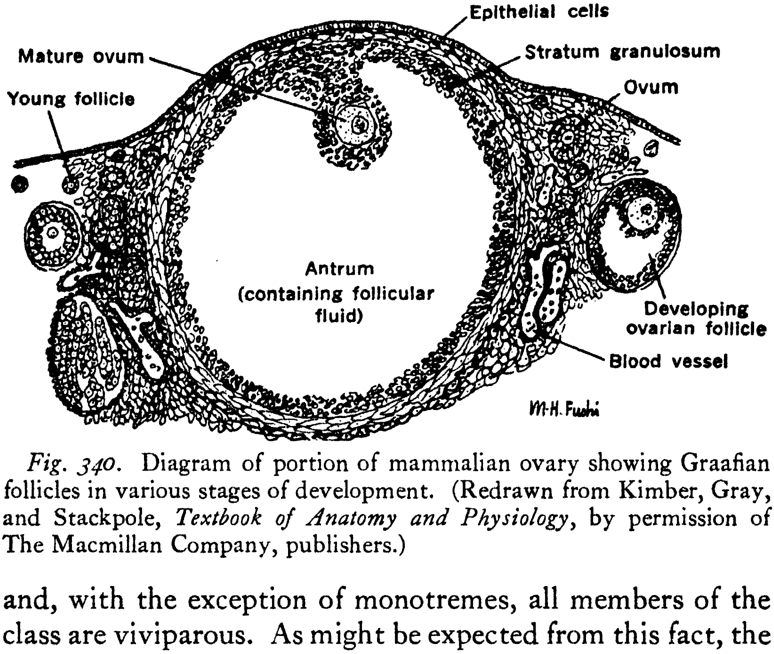


Fig. 340. Diagram of portion of mammalian ovary showing Graafian follicles in various stages of development. (Redrawn from Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, by permission of The Macmillan Company, publishers.)

In typical mammals the ovaries are small, round, solid bodies which remain in the median dorsal portion of the abdominal cavity. Inside the ovary, the ovum develops within a small group of cells known as the Graafian follicle (Fig.

340). The Graafian follicle is a spherical mass of cells with a crescent-shaped cavity forming within in such a way that the ovum is surrounded by a double wall of cells. With the maturing of the ovum, the Graafian follicle moves to the surface of the ovary and eventually ruptures, liberating the egg into the body cavity. The remains of the Graafian follicle on the surface of the ovary become filled with a blood clot which is later replaced by a mass of lutein cells which form the corpus luteum. This structure, which has an endocrine function, will be described in a subsequent chapter.

It was stated above that the ovum is set free in the body cavity. Although there is no morphological connection between the oviduct and ovary in most mammals, the expanded open end of the duct (ostium) is in such close proximity to the ovary, in some cases partially surrounding it, that there is little possibility of the eggs being lost in the coelom. The oviduct in the mammals also is a Mullerian duct. The posterior portion enlarges to form the uterus, within which the embryo develops. In many mammals the two uteri coalesce posteriorly to form a single vagina. Much variation is found in this region, not only in the structure of the organs but also in their relation to the excretory system.

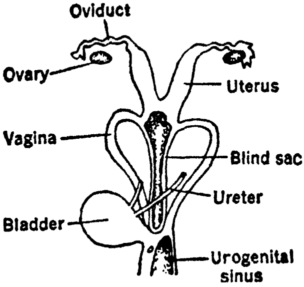
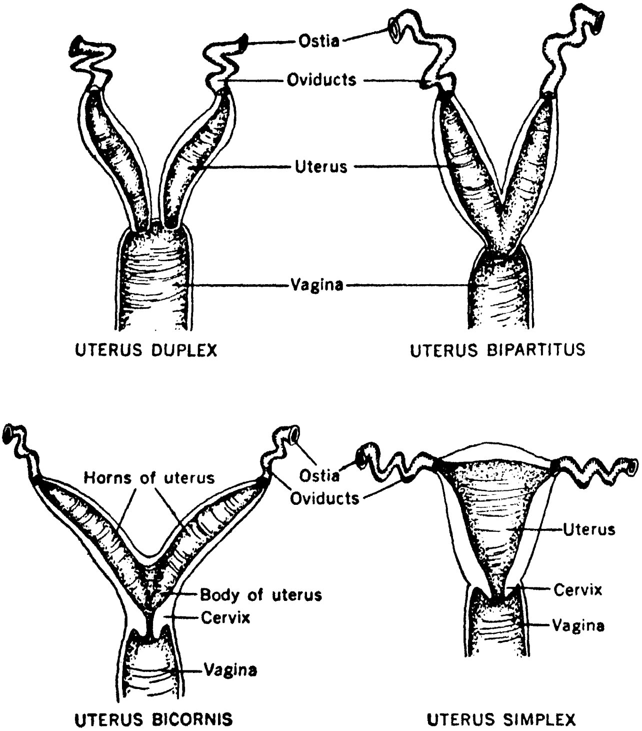


Fig. 341. Female sexual apparatus of the kangaroo, showing the double vagina. (From Walter, *Biology of the Vertebrates*, after Gegenbaur, by permission of The Macmillan Company, publishers.)

In the monotremes the two uteri (really oviducts in this egg-laying mammal) empty separately into the urogenital sinus near the openings of the excretory ducts. The urogenital sinus empties into a cloaca. In the marsupials, the ducts remain separate, but a uterus and a vagina develop on each side. The latter open into a urogenital sinus which opens externally separate from the anus. In this order there is found not only a duplex uterus but also a duplex vagina (Fig. 341), and a urogenital opening quite distinct from the anus.

In the placental mammals the terminal portions of the oviducts unite to form a single vagina. Much variation is seen in the extent to which the uterine regions of the oviduct unite (Fig. 342). In some mammals, such as the rabbit, beaver, and elephant, the two oviducts do not unite, each



UTERUS DUPLEX UTERUS BIPARTITUS UTERUS BICORNIS UTERUS SIMPLEX

Fig. 342. Diagrams showing types of uteri in mammals. The ventral surface is largely removed to show internal structures. (Redrawn from Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

opening separately into the single vagina. This is known as the duplex type of uterus. In some ungulates, in many carnivores, and among certain bats and rodents, the most posterior portions of the oviducts unite. This results in the formation of the bipartite uterus, one in which the cavity is partially divided by an internal partition, but which has a single opening into the vagina. In the bicornuate type of uterus, found in many ungulates, in bats, and in the cetaceans, the uterus consists of an enlarged posterior cavity with two uterine horns leading into it. In this type a relatively larger portion of the oviducts function as a uterus.

In the primates, including man, the simplex type of uterus is characteristic. The simplex uterus consists of a single large cavity showing little trace of its double origin. The two small oviducts (Fallopian tubes) enter its anterior and lateral margins.

The vagina is that part of the united oviducts, posterior to the uterus, which receives the male copulatory organ (penis). As mentioned above, a vagina is not present in the monotremes, while in the marsupials it is a double organ. In placental mammals, a single vagina is present. This, in many mammals, is joined posteriorly by the excretory duct (urethra) from the bladder to form a common urogenital cavity, the vestibule. The vestibule leads to the external opening. In some cases, as in the rat, the urethra does not unite with the vagina to form a vestibule. It continues posteriorly to the urinary opening, which is anterior and ventral to the opening of the vagina.

In most primates, the opening of the shallow vestibule is bounded laterally by two integumental folds, the labia minora (Fig. 343). Lateral to these and more external in the higher primates, are two larger folds, the labia majora. Anterior to the urethra and between the labia minora is a small body, the clitoris. This is the homologue of the penis in the male.

Associated with the reproductive organs of the female are various glands. Among these may be mentioned glands in the wall of the uterus which secrete a mucus which moistens the inner surface of the vagina. In the human being the glands of Bartholini, located at the junction of the urethra and the vagina, secrete a mucus which serves as a lubricant during copulation.

The placenta, a structure characteristic of most mammals, may well be mentioned here, as it plays such an important part in the embryonic development of this group of animals (Fig. 344). The placenta is a highly vascular organ consisting of villi from the uterine wall and from the outer surface of the chorion. Through the surfaces of these villi intimate relations are established between the embryonic and the maternal circulatory systems, thereby facilitating the exchange of digestive, respiratory, and excretory materials.

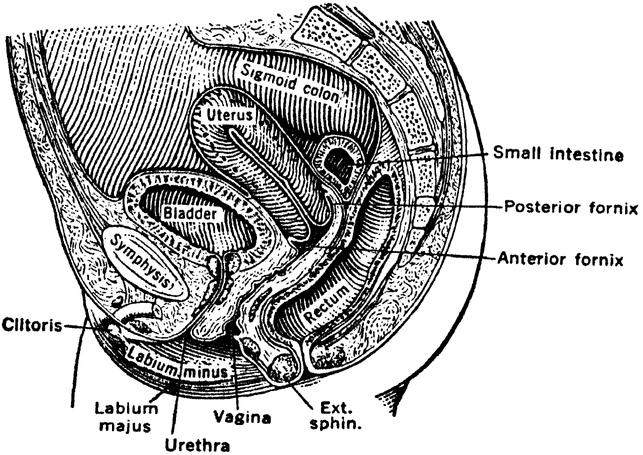


Fig. 343. Sagittal section of the human pelvis (female). (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, by permission of The Macmillan Company, publishers.)

The gonads of the male mammal develop in much the same manner and in the same region of the body as do the ovaries. In many mammals, however, they do not remain in their original position, but instead descend (posteriorly) through the abdominal cavity and take up their position in a sac of skin and muscle, the scrotum (Fig. 345). The cavity within the scrotum is a part of the coelom, from which it was formed. In the monotremes, cetaceans, and proboscidians, and in many insectivores, the descent of the testes does not take place. In other types, as in the rodents and bats, there is a temporary descent associated with periods of sexual activity. In most carnivores, the ungulates, and primates, the descent results in a permanent change of position. In certain cases where the descent is permanent, as in the rhinoceros, the testes lie just beneath the integument of the region rather than in a definite scrotum. In those species having a tempo-

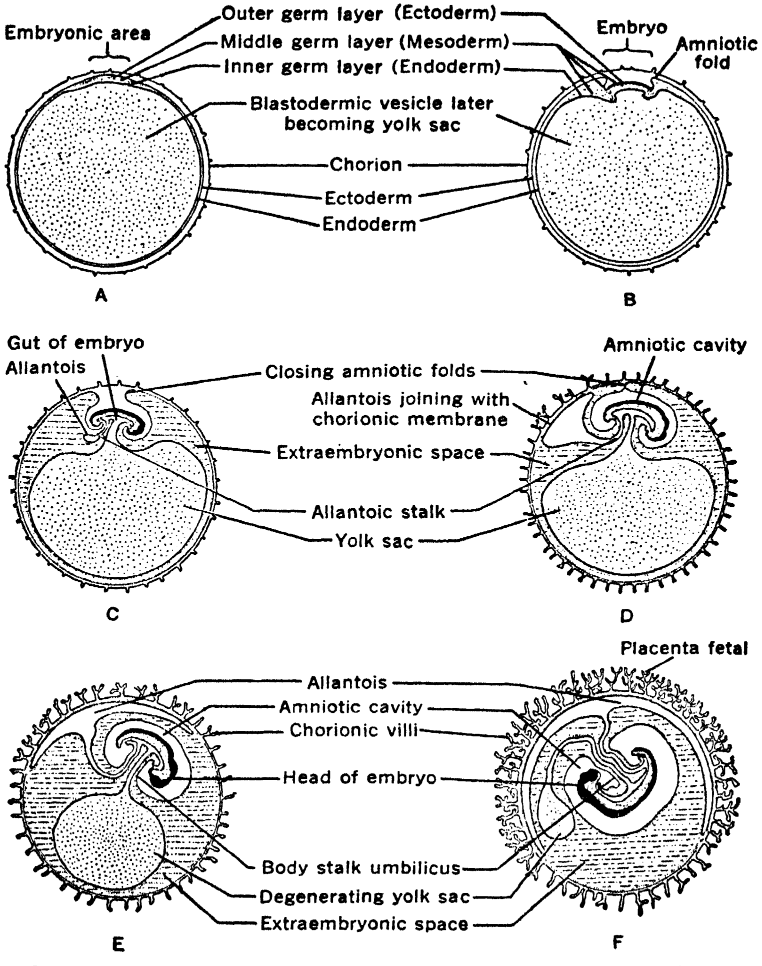


Fig. 344. Diagrammatic sections showing the development of the egg and embryonic membranes of a mammal. A, blastula showing beginnings of embryo at top, before the appearance of the amnion; B, embryo outlined, with developing amnion and yolk sac; C, embryo with amnion further developed and allantois appearing; D, embryo with amnion closing, and allantois joining with outer membrane, or chorion; E, F, embryos in which the vascular layer of the allantois is applied to the chorion and growing into the villi of the latter to form the fetal placenta; yolk sac reduced; amniotic cavity increasing; mouth and anus established. (From Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

rary descent, a narrow passage way, the inguinal canal, remains connecting the cavity of the scrotum with the coelom.

The testis of the typical mammal is an oval body divided internally by connective tissue partitions into numerous triangular cavities (Fig. 346). Within these cavities are located the seminiferous tubules inside of which the germ cells develop. In the spaces between the seminiferous tubules, groups of interstitial cells may be seen (Fig. 347). These cells have an endocrine function which will be referred to later. Within the testis the tubules are convoluted, but straighten out as they converge and leave the testis as the vasa efferentia. These are continuous with the tubules of the epididymis, which, it should be recalled, are remains of the anterior portion of the mesonephric kidney. The epididymis consists of three parts, the caput, corpus, and cauda epididymis. The latter continues as the vas deferens, the genital duct which was the mesonephric, or Wolffian, duct.

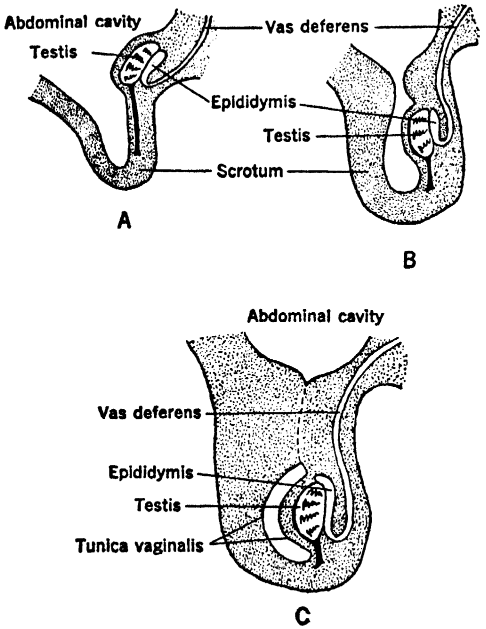


Fig. 345. Three stages in the descent of the testes. (Redrawn from Walter, *Biology of the Vertebrates*, after Arey, by permission of The Macmillan Company, publishers.)

The vasa deferentia unite with the urethra, which, from this point on, becomes a urogenital duct. This urogenital duct continues through the penis, the copulatory organ of the male, to the external opening at the end of the penis.

Much variation in the penis is seen within the class Mammalia (Fig. 348). In the monotremes, it is still largely reptilian in form and function. The urogenital sinus is located anterior to the penis and opens directly into the cloaca. It is ordinarily urinary in function. The penis is a grooved structure slightly erectile and only slightly protrusible from the cloaca. Upon erection, the groove becomes a closed tube, and the normal opening of the urogenital sinus into the cloaca is closed. The sperm cells, therefore, must pass through the canal of the penis into the cloaca of the female.

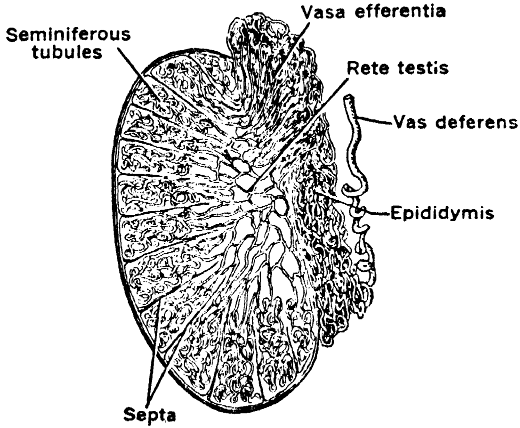


Fig. 346. The human testis, semidiagrammatic. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

In the marsupials, with the loss of the cloaca, the penis is an external structure having a closed tubular urogenital canal. The penis is here directed posteriorly with the testes located anterior to it.

The penis of placental mammals is not essentially different from that of the marsupials except that it is located in front of the testes and is usually directed anteriorly. In the cat and many rodents, it is directed posteriorly except during copulation. In some mammals it is withdrawn inside a protective sheath, except during sexual activity.

Internally the mammalian penis (Fig. 349) consists of two elongated masses of erectile tissue, the corpora cavernosa. These lie side by side, with a third mass of tissue, the corpus spongiosum, beneath them. Surrounding these bodies is a layer of connective tissue and the loosely fitting skin. The urethra extends through the corpus spongiosum to the end of the penis. In most mammals the penis terminates in an enlarged portion, the glans. This, in the higher mammals, is covered by a double fold of skin, known as the prepuce. In many mammals the penis is made more rigid by the presence of a bone, the os priapi, between the corpora cavernosa.

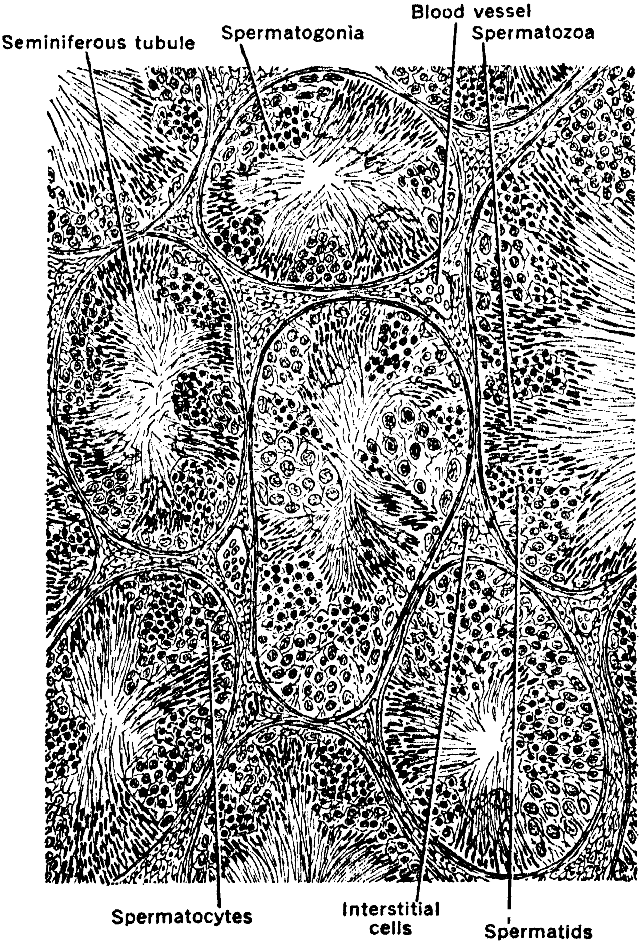


Fig. 347. A section of the testis of the frog. (From Huettner, *Fundamentals of Comparative Embryology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

In the male as in the female, various glands are found along the genital ducts. The more constant of these are the seminal vesicles (vesicular glands), the prostate, the glands of Littre, and Cowper's glands. The vesicular glands are a pair of sac-like bodies at the end of the sperm duct. Although sperm cells may be found within them, they have a glandular rather than a storage function. The prostate, the largest of the accessory glands, surrounds the base of the urethra. Its secretion, a thin, milky fluid, is carried to the urethra by several ducts which enter the urethra near the entrance of the vasa deferentia. The glands of Littre are mucous glands in the dorsal wall of the urethra in the penis, while Cowper's glands are two small bodies with ducts opening into the urethra at the base of the penis. These various glands in the male

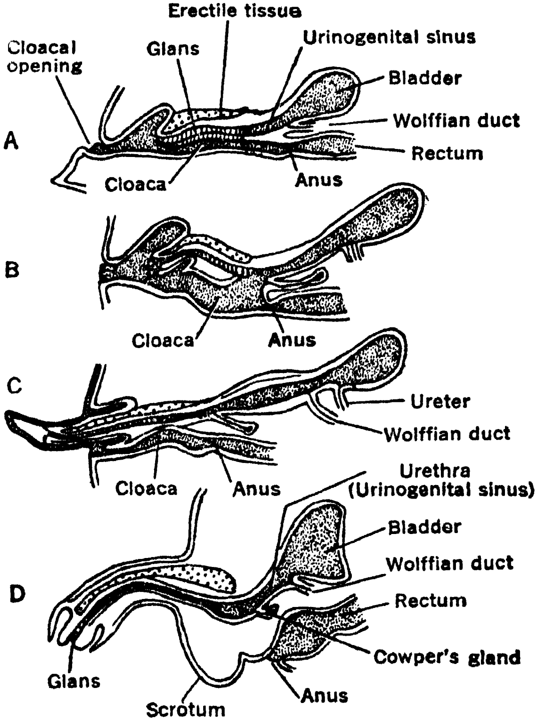


Fig. 348. Stages in the evolution of the penis. A, tortoise; B, spiny anteater; C, kangaroo; D, man. (Redrawn from Walter, *Biology of the Vertebrates*, after Keith, by permission of The Macmillan Company, publishers.)

secrete the different fluids which together make up the spermatic fluid, a liquid medium providing for the locomotion of the sperm cells.

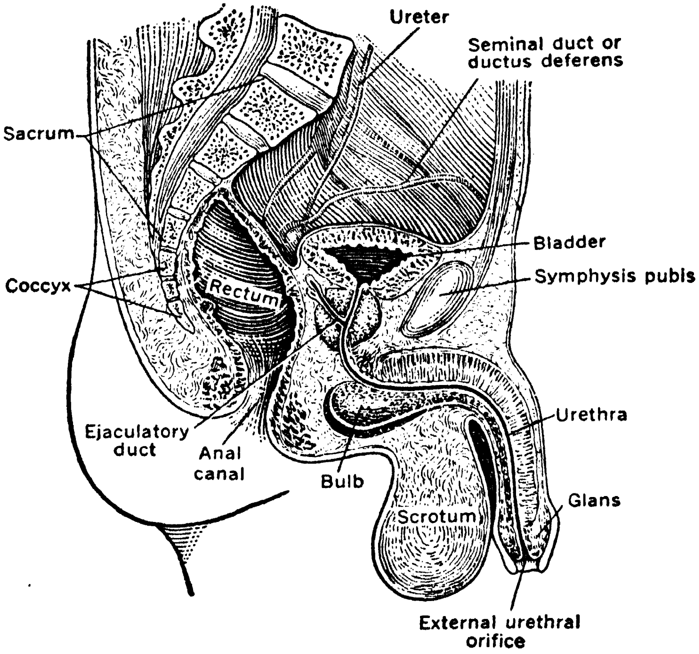


Fig. 349. Sagittal section of the human pelvis (male). (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, by permission of The Macmillan Company, publishers.)

SUMMARY

The reproductive system provides for the perpetuation of the race, while the other systems are concerned with the life of the individual member of the race. The reproductive system includes the germ cells, the gonads, various structures which insure fertilization and other structures in which the fertilized egg undergoes development.

The germ cells are the sperm of the male and the ovum of the female. These undergo development or maturation in the gonads, which are in the male the testis, and in the female the ovary. Among the structures insuring fertilization are the genital ducts, copulatory organs, and various glands. A variety of structures such as shell glands, uteri, integumental pouches, embryonic membranes, and mammary glands aid in the care of the fertilized egg, the embryo or the young.

In the cyclostomes the germ cells of both sexes are liberated into the coelom and then pass through genital pores into the urogenital sinus. This opens externally by way of the urogenital pore, located just posterior to the anus.

In elasmobranch fishes sperm cells pass from the testes through the tubules of the anterior portion of the mesonephros into the Wolffian duct. The Wolffian ducts unite to form a urogenital sinus which opens into the cloaca. In the female the oviducts are not related to the ovaries or to the excretory ducts. The ova pass from the ovaries through the coelom into open ends of the oviducts. The latter open separately into the cloaca. In teleostomous fishes the gonads often unite so that there is a single genital duct leading to the external opening. This duct, in the male, may or may not unite with the excretory duct. In the female the ovaries are frequently directly connected to the oviducts which lead to the external opening.

The amphibian system is very similar to that of the elasmobranch fishes. In the male the sperm cells pass through the anterior part of the mesonephros into the Wolffian duct and in the female the ova pass through the coelom on their way into the open ends of the oviducts.

In forms above the amphibians, the remains of the mesonephric kidney and the Wolffian duct in the male are associated with reproduction only, as the metanephros has become the functional kidney. In the female vestiges of the mesonephros remain. Copulatory organs, or penes, are present in reptiles and mammals. In viviparous reptiles and in all mammals except the monotremes, the posterior ends of the oviducts enlarge to form a uterus, in which the fertilized egg undergoes development.

The presence of the embryonic membranes has made possible the development of the embryo outside a water environment. In the placental mammals, the placenta provides for the exchange of nutritive materials and wastes.

XIV. The Nervous System

FUNCTIONS

In the preceding chapters the morphology of the vertebrate body has been described in terms of the different systems of organs. It has been shown that each of these systems has its own definite part to play in the life of the individual animal. It should be kept clearly in mind, however, that none of these systems are functioning units operating entirely by themselves and independently of the others. The vertebrate body does not consist of a series of organ systems that can be considered as either morphologically or physiologically distinct from one another. Not only must the different organs of any one system work together in performing the functions of that system, but also the activities of all the systems of the body must be coordinated in the performance of those varied duties necessary to normal and healthy animal life.

This necessary coordination of the various systems within the vertebrate body is brought about by the activity of two different groups of organs: namely, those making up the nervous system and those comprising the ductless, or endocrine, glands. The nervous system is a conducting mechanism which has often been compared to a telephone system. With the aid of the sense organs stimuli of various kinds are received from the environment, the resulting nerve impulses are transmitted to the central office, the brain, for interpretation or adjustment, and then relayed to the proper destination — some organ which responds in a definite way to the given stimulus. The exact nature of nerve conduction has not yet been satisfactorily determined. The part played by the nervous system in coordinating the activities of the body may be either voluntary or involuntary.

The various endocrine glands, which will be described more fully in the following chapter, bring about definite chemical regulation which is involuntary in character. Both kinds of coordination, nervous and endocrine, depend primarily upon that property of irritability that is characteristic of protoplasm. By irritability is meant the tendency of protoplasm to respond in a definite way to a given stimulus. The sense organs are specialized for the reception of stimuli: the parts of the nervous system, for the conduction of the nerve impulses resulting from the stimuli, to their proper destinations.

UNITS OF THE NERVOUS SYSTEM

The unit of structure of the nervous system is the nerve cell, or neuron. A nerve cell differs in appearance from other animal cells in having the cytoplasm drawn out into long and slender processes (Fig. 350). The body of a neuron contains a typical nucleus. Through the endings of their cytoplasmic processes, contacts (synapses) are made between neurons. In this way a network of contacting fibers is established, which in its various ramifications reaches all parts of the body. Thus, a relation is established between the most remote organs and the externally located sense organs, which are subject to the various types of stimuli.

As indicated above, a neuron is a highly specialized conducting cell (Fig. 351). Typically, the direction of conduction is definite in a given cytoplasmic process. Those processes in which the direction of conduction is away from the body of the neuron are known as axons. The others, which conduct impulses to the body of the nerve cell, are the dendrites. Obviously each neuron must have at least one axon and one dendrite. Such a cell is a bipolar neuron. A large number of nerve cells, however, have more than one dendrite and are therefore called multipolar neurons.

A neuron consists of a cell body and a number of cytoplasmic processes. The body, or cyton as it is now called, consists of a mass of granular cytoplasm within which is a typical nucleus. Numerous fine fibrils form a network within the cyton and extend into the dendrites and axons. These are known as neurofibrils. They make up almost the entire axon. Scattered about in the cyton and in the larger dendrites are the so-called Nissl bodies. These bodies contain a substance which stains deeply with certain basic dyes. They are considered to be storehouses of energy which play a part in the metabolism of the neuron.

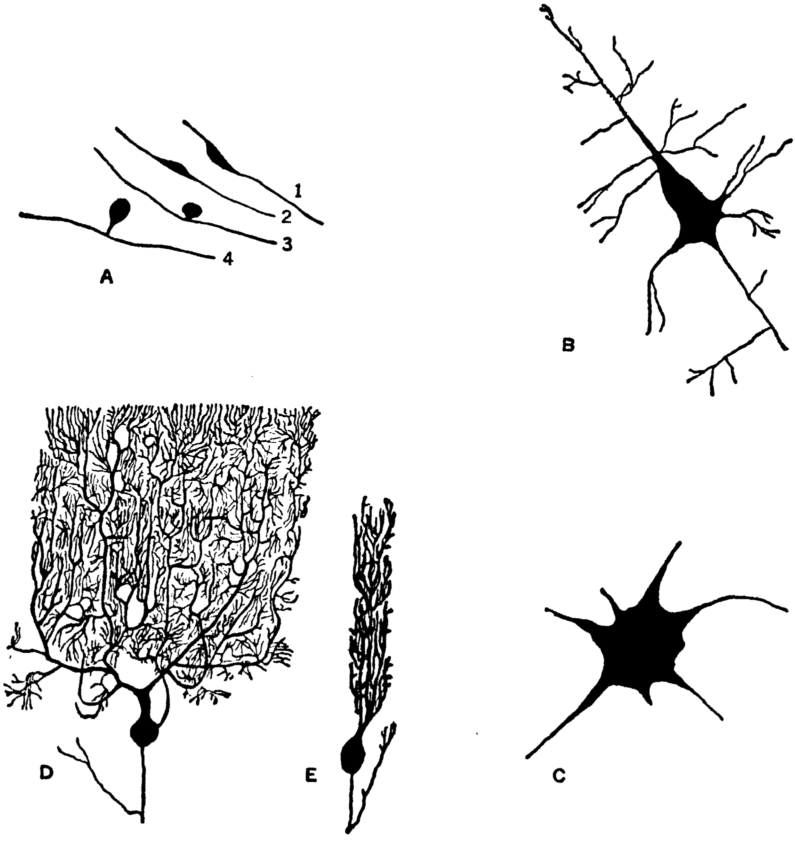


Fig. 350. Types of neurons. A, cell of dorsal root ganglion; 1,2,3,4 show how it gradually develops into a unipolar cell. B, pyramidal cell of cerebral cortex. C, motor cell of spinal cord. D and E, Purkinje cells of cerebellum; E, lateral view. (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, by permission of The Macmillan Company, publishers.)

The processes of a neuron are subject to much differentiation. Axons may attain a great length, sometimes being equal to half the length of the body. Their surfaces are smooth and their diameter decreases very little throughout their length. There is usually a single axon to each nerve cell. They may give off several tiny branches, which are known as collaterals. Dendrites, on the other hand, are relatively short and thick at the base. Their surface is rough and the diameter decreases away from the cell body. They

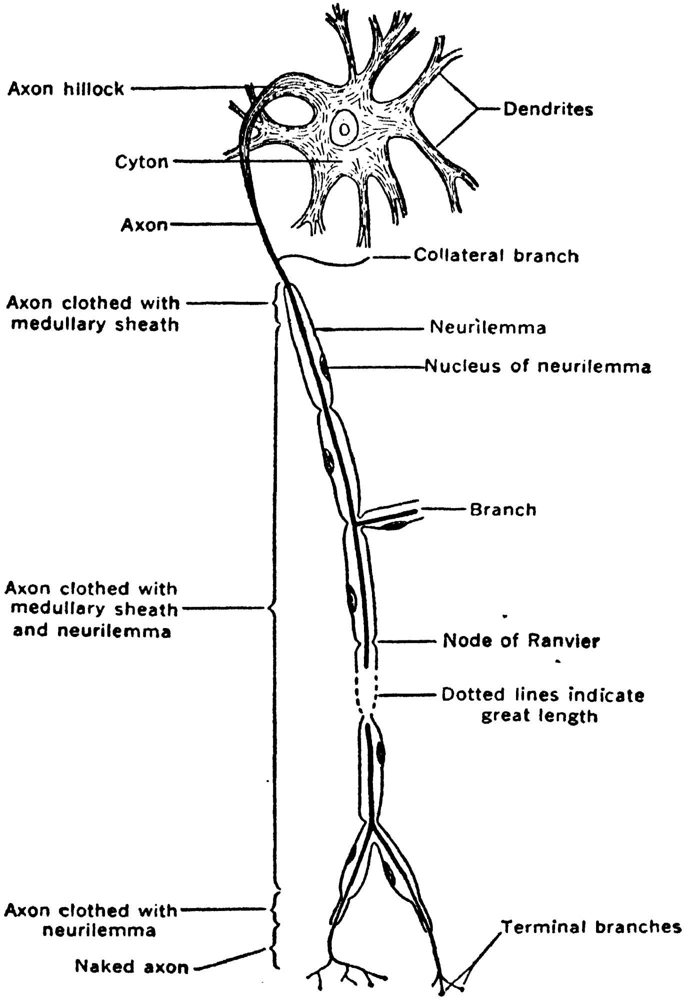

Axon hillock
Dendrites
Cyton
Axon
Collateral branch
Axon clothed with medullary sheath
Neurilemma
Nucleus of neurilemma
Branch
Axon clothed with medullary sheath and neurilemma
Node of Ranvier
Dotted lines indicate great length
Axon clothed with neurilemma
Terminal branches
Naked axon

Fig. 351. A motor neuron from the nerve cord. (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, by permission of The Macmillan Company, publishers.)

give rise to many side branches and their number in a given neuron varies.

The nerve processes are surrounded by various sheaths. A cross section of a nerve fiber may show three parts. In the center is the cell process which is called the axis cylinder. Surrounding this is the medulla or myelin sheath which is composed of a fatty, semifluid substance. It is this sheath which gives to a nerve fiber its white color. Just outside the myelin sheath is a thin membrane, made up of elongated cells, called the neurilemma. This completely invests the nerve fiber and forms its outer covering. In fibers of this type the myelin sheath is interrupted at intervals and the neurilemma is brought close to the axis cylinder. These constrictions are known as the nodes of Ranvier. They are thought to be for the purpose of allowing tissue fluid to bathe the nerve fiber for nutritive purposes. The myelin sheath is considered to be an insulator of the fiber, preventing the loss of the nerve impulse. The nuclei of the neurilemma cells take part in the regeneration of fibers which may be cut off from their cytons. Nerve fibers of this type are said to be medullated.

Nonmedullated fibers are those which show a great reduction or absence of the myelin sheath. In this kind the neurilemma immediately invests the nerve fiber. Such fibers are gray or yellow in color because of the absence of the myelin sheath. Cells of the sympathetic ganglia have fibers of this type. The presence or absence of the myelin sheath is the factor which is responsible for the difference between the white and gray matter of the brain and nerve cord.

It is now generally considered that the neurons act as separate units in the conduction of a nerve impulse. There is probably no continuity of protoplasm between two neurons, but merely a contact between them. The branches of the axon of one neuron may touch the surface of the cyton of another neuron, or they may form a network with its dendrites. This contact between two neurons is known as a synapse. It is possible that the membranes at the synapse increase the resistance to nerve impulses or initiate new ones.

Associated with the neurons in the formation of nerve tissue in the brain and nerve cord are supporting nonnervous cells collectively known as neuroglia. These cells also are of ectodermal origin.

The units of the nervous system may also be classified according to the type of activity performed by them. On this basis may be distinguished sensory, motor, and association neurons. The sensory neurons are those which first receive the nerve impulse from the sense organ. Motor neurons are those nerve cells which finally deliver the interpreted nerve impulse to some organ which responds in a definite manner. Between a sensory and a motor transmitter a varying number of association neurons may serve as relayers of the given impulse.

A still further distinction may be made in the case of both sensory and motor neurons. Both kinds may be subdivided into somatic and visceral neurons, according to the exact nature of their activities. Somatic sensory and somatic motor neurons are in general concerned with those voluntary activities of an organism brought about in response to external stimuli; visceral sensory and visceral motor, on the other hand, are concerned with activities of the organs of the body which are in general caused by internal stimuli of a chemical nature. Since the nervous system is concerned with coordination of all the activities of the body, it is obvious that there could not be a hard and fast line of demarcation between these kinds of neurons, either from an anatomical or a physiological standpoint.

It will thus be seen that, while the unit of function as well as of structure is the nerve cell, in the vertebrates a single neuron does not function as both sensory and motor transmitter in any given activity of the nervous system. There must be at least one of each type of neuron between the sense organ and the responding organ. Usually between the sensory and motor transmitter there is at least one association neuron. It is customary, therefore, to consider the so-called reflex arc (Fig. 352) as the functional unit of the nervous system. A typical reflex arc consists of the following parts:

1. The receptor — a sensory cell or sense organ.
2. The sensory transmitter — a sensory neuron.
3. The relaying transmitter — one or more association neurons.
4. The motor transmitter — a motor neuron.
5. The effector — the responding organ, such as a muscle or gland.

In the simplest type of reflex the third element, the association neuron, is not present.

The bodies of nerve cells make up the gray matter of the nervous system. The bundles of medullated fibers form the white matter.

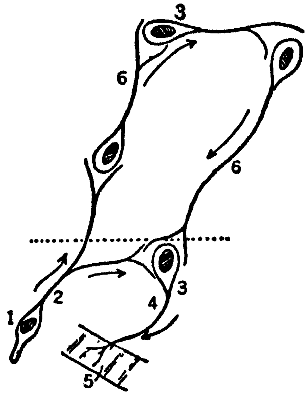


Fig. 352. The plan of a reflex arc. 1, receptor; 2, sensory transmitter; 3, adjustor; 4, effector transmitter; 5, effector; 6, relayer. Below the dotted line is represented a simple reflex; above, a more complicated reflex involving more neurons. (From Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

EMBRYOLOGY

The beginning of the nervous system in vertebrates may be traced back to a very early stage in the development of the embryo (Fig. 3). Near the end of the gastrula stage a thickening of ectoderm takes place in the median dorsal region of the embryo. This is known as the medullary plate. Later the edges of this elongated plate grow dorsally, forming a shallow medullary groove. This dorsal growth of the edges of the groove continues and is eventually directed medially until the edges come together in the median line to form a closed medullary tube. The closure of the tube first becomes complete in its middle portion and gradually extends toward both ends. The hollow neural tube thus formed eventually becomes separated from the external surface as other tissues develop above it.

As the neural tube closes in the median line, lateral ridges of neural (medullary) tissue form in the angles between the region of closure and the ectoderm of the skin. These are the neural crests, which later separate from the neural tube and break up into segmentally arranged bodies which form the spinal ganglia. From the neural tube and these spinal ganglia eventually develop the various kinds of neurons mentioned above, which constitute the peripheral portions of the nervous system. By various mechanisms of growth in different regions of the tube, the various parts of the system characteristic of the vertebrates are developed.

PARTS OF THE SYSTEM

It is customary to divide the vertebrate nervous system into three parts, the central, the peripheral, and the autonomic. The central nervous system includes the brain and the nerve cord (Fig. 353); the peripheral consists of the paired cranial and spinal nerves which respectively connect the brain and cord with the other organs of the body; and the autonomic system includes those neurons associated with the involuntary activities of the viscera. Obviously these are not separate systems functioning independently of one another, but are connected parts of one system.

As was mentioned above, the gray matter is composed of cell bodies and the white matter of cytoplasmic processes extending from the cell bodies. In the nerve cord, the gray matter is inside; the white matter on the outside. In the brain the relation is reversed, the gray matter being external to the white.

A group of cell bodies forming a definite mass outside the brain and cord is known as a ganglion. A similar aggregate of bodies within the central nervous system is a nucleus, or center. A strand made up of a number of cytoplasmic processes extending up or down within the nerve cord or brain is a tract, while a similar bundle of fibers outside the central nervous system is a nerve.

The Central Nervous System

The brain and cord develop from the medullary tube. The original tubular character is retained in the adult in vertebrates generally, the cavity remaining as the central canal of the nerve cord and the ventricles of the brain. The anterior portion enlarges to form the brain; the remainder, or nerve cord, retains much of its original appearance. Because of its greater simplicity of structure, the nerve cord will be described first.

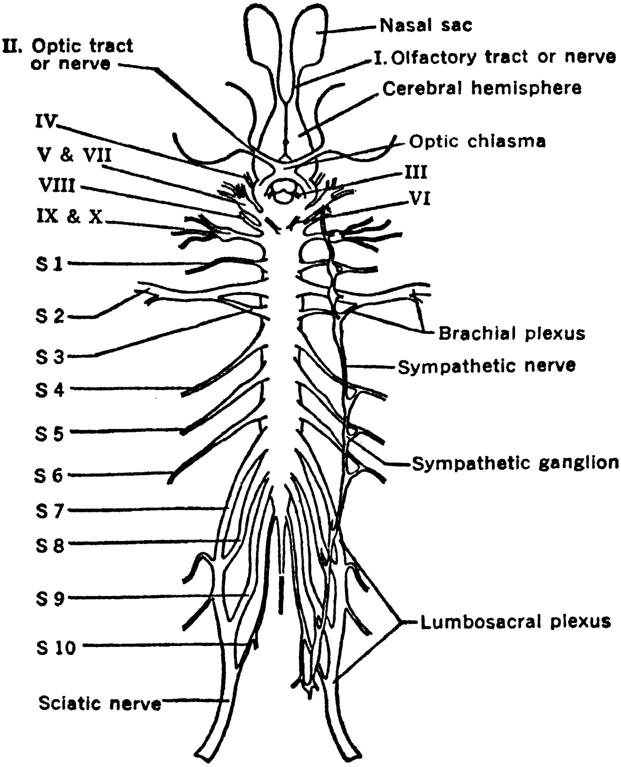


Fig. 353. Diagram of the central nervous system of the frog, showing the origin of the cranial and spinal nerves. (From Mavor, *General Biology*, by permission of The Macmillan Company, publishers.)

THE NERVE CORD. The development of the nerve cord in a majority of vertebrates is accompanied by a greater growth of its lateral walls as compared with those dorsal and ventral to the central canal. As a result, longitudinal furrows, or grooves, are formed in the median dorsal and ventral surfaces. These are known, respectively, as the dorsal sulcus and the ventral fissure. In mammals particularly, other shallower longitudinal grooves appear on the surface of the cord, giving it a fluted appearance.

The length of the nerve cord is subject to much variation in the different vertebrates, its extent being influenced by a number of factors. With the greater development of the brain may be noticed a roughly corresponding shortening of the cord. In man the nerve cord is approximately eighteen inches in length, reaching only to the region of the first lumbar vertebra. In only a few mammals does the cord reach as far posteriorly as the sacrum.

The absence of the tail, as in the anurans, has resulted in the shortening of the cord as compared with that of their close relatives, the urodeles. In the frog there are but ten pairs of spinal nerves. The extreme case of reduction of the nerve cord is seen in that strange teleost fish *Orthagoriscus*, in which the cord is slightly shorter than the brain itself.

In those vertebrates which do not have extensive development of the paired limbs, the nerve cord tapers gradually to its posterior end. In other forms, where the appendages are well developed, there is a noticeable thickening of the cord in the corresponding regions. These are the cervical and lumbar enlargements. In *Amphioxus* and in such forms as eels, snakes, legless amphibians, and legless lizards, these enlargements are not present. In the kangaroo, the lumbar enlargement is much greater than the cervical, while in the bats and flying birds the reverse is the case. The greatest development of these enlargements probably occurred among the extinct group of dinosaurs, many of which showed excessive development of the hind limbs. In several of these species, the lumbar enlargements were probably several times as large as the brain.

In those vertebrates having a short nerve cord, it tends to narrow abruptly and then continue as a tapering thread of nonnervous tissue, the filum terminale (Fig. 373). In cases where the cord ends anterior to the hind limbs and to other structures which must be innervated, the spinal nerves supplying these organs leave the cord and pass to these organs more or less parallel to one another, as well as to the cord itself. This forms a brushlike bundle of nerves known as the cauda equina.

There is also much variation in the internal structure of the nerve cords of different vertebrates as shown by their cross sections. As was stated above, in the nerve cord the gray matter is within the white matter. In many lower vertebrates, the distinction between the gray and white matter is very indefinite. Beginning with the higher fishes, this distinction becomes more and more apparent.

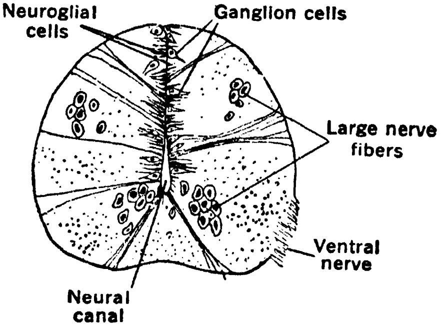


Fig. 354. Cross section through the nerve cord of *Amphioxus*. (From Walter, *Biology of the Vertebrates*, after Haller, by permission of The Macmillan Company, publishers.)

In *Amphioxus* (Fig. 354), the cord is roughly triangular in outline and there are no longitudinal furrows. In the cyclostomes (Fig. 355), it is widened laterally with a convex dorsal and a concave ventral surface. In the fishes (Fig. 356), a dorsal fissure is present, and the cord is more rounded in cross section. In the amphibians, both dorsal and ventral fissures are apparent, and the cord is more oval or elliptical in outline. The cord in reptiles and birds is essentially similar in form to that of the amphibians, except for a clearer demarcation between gray and white matter.

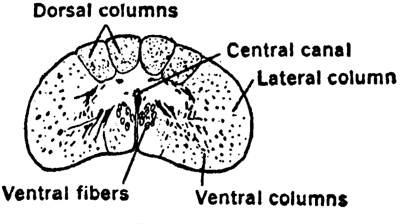


Fig. 355. Cross section through the nerve cord of the lamprey eel, *Petromyzon*. (From Walter, *Biology of the Vertebrates*, after Haller, by permission of The Macmillan Company, publishers.)

The mammalian nerve cord is roughly circular in outline with a deep dorsal sulcus and a wider ventral fissure (Fig. 357). The gray matter is in the form of an H with the dorsal and ventral roots of the spinal nerves continuous with the two lateral limbs of the H. The crossbar connecting the limbs is the gray commissure. The small central canal is located near the ventral margin of the crosspiece. The gray matter of each half of the cord divides the white matter into three separate regions, the funiculi. We thus have a dorsal, a lateral, and a ventral funiculus.

That portion of the gray matter continuous with the dorsal roots of the spinal nerves is the dorsal cornu. A corresponding part continuous with the ventral roots is the ventral cornu. Between the two cornua is the lateral column. Through the dorsal cornua the fibers from sensory neurons enter the cord. The bodies of these sensory neurons are located in the dorsal ganglia. Passing out of the cord by way of the ventral cornua are fibers from motor neurons whose bodies are located within the gray matter of the cord.

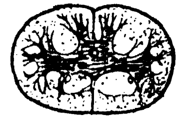


Fig. 356. Cross section through the nerve cord of a teleost fish, *Salmo.* (From Walter, *Biology of the Vertebrates,* after Butschli, by permission of The Macmillan Company, publishers.)

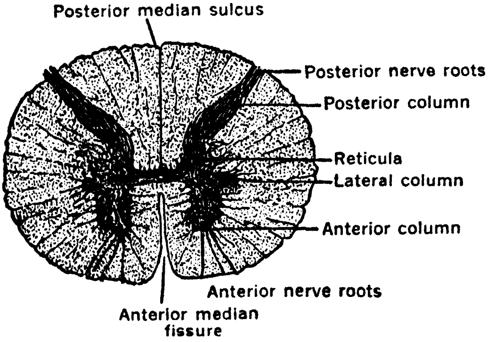


Fig. 357. Cross section of human nerve cord at the middle of the thoracic region. (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology,* after Gerrish, by permission of The Macmillan Company, publishers.)

The funiculi are made up of columns composed of fibers which are either ascending from various levels of the cord to the brain, or descending from the brain to different levels of the cord. These columns, or tracts, have been quite definitely mapped out in the human nerve cord, so that the character of the fibers contained in each has been determined. The columns in the dorsal funiculi are ascending sensory tracts. The lateral and ventral portions of the lateral funiculi and the lateral half of the ventral funiculi also contain ascending sensory tracts. The median portion of the lateral funiculi contains the so-called ground bundles, in which are located association neurons. These neurons, which are located entirely within the limits of the cord, form connections between other neurons. The chief descending motor tracts are found in the columns known as pyramidal tracts. One of these is located in the dorsal half of the lateral funiculus between the ascending sensory tract and the ground bundle. The other is at the side of the ventral fissure in the ventral funiculus.

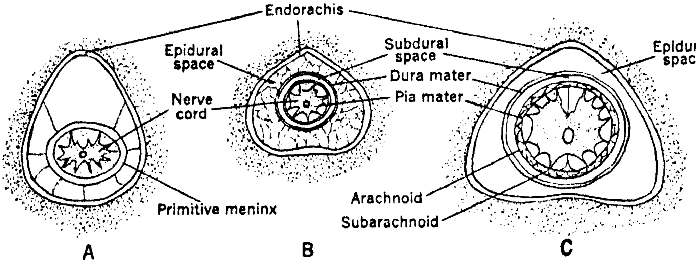


Fig. 358. Diagrams of the meninges in the chief groups of vertebrates. A, fishes; B, amphibians, reptiles, and birds; C, mammals. (Redrawn from Walter, *Biology of the Vertebrates*, after Sterzi, by permission of The Macmillan Company, publishers.)

ENVELOPES OR MENINGES. The nerve cord and brain are covered with protective membranes of connective tissue, known as meninges (Fig. 358). In the fishes, as in the embryos of higher forms, a single envelope, the primitive meninx, is present, closely applied to the surface of the cord. This is surrounded by a fluid-filled space which separates it from a thin tissue, the endorachis, which lines the neural canal, through which the cord passes. In amphibians, reptiles, and birds, the primitive meninx splits, forming the inner pia mater and the outer dura mater, which are separated by the subdural space. In the mammals, the innermost meninx (pia mater) divides, giving rise to the arachnoid (outer layer) and the pia mater (inner layer). The space between these is known as the subarachnoid space. Like the other spaces, this is filled with a lymphlike cerebrospinal fluid. In those vertebrates having a dura mater it is separated from the endorachis by a similar space, the epidural.

The meninges of the brain are essentially similar to those surrounding the cord. A noticeable difference, however, is that within the cranium of mammals there is no epidural space, as the dura mater and endorachis are continuous.

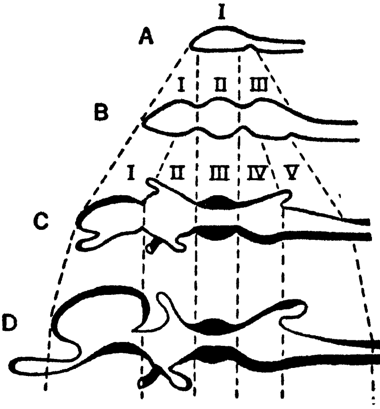


Fig. 359. Diagrams of the encephalon and its evolution. A, primitive encephalon; B, division into prosencephalon, mesencephalon, and rhombencephalon; C and D, further division into the five regions of the brain. (From Walter, *Biology of the Vertebrates*, after Roule, by permission of The Macmillan Company, publishers.)

THE BRAIN. The anterior end of the medullary tube is further modified to form the brain. The progressive specialization of the brain from the lower to the higher animals is closely correlated with the increase of cephalization, resulting in the localization of the important organs of special sense in the head region. The great importance of the brain as a part of the nervous system is in the association centers which bring about coordination and adjustment of the incoming sensory and outgoing motor impulses. The dominant position occupied at the present time by mammals in general and man in particular has been very largely due to their greater development of these associative areas of the brain.

Embryology. After the closure of the neural tube, the anterior end of the cord enlarges to form the primary vesicle of the brain, which is called the encephalon (Fig. 359). At an early stage of development, as a result of unequal growth in its various parts, this encephalon becomes partially divided into three regions. This forms the so-called primary brain which consists of forebrain, midbrain, and hindbrain, or the prosencephalon, mesencephalon, and rhombencephalon respectively.

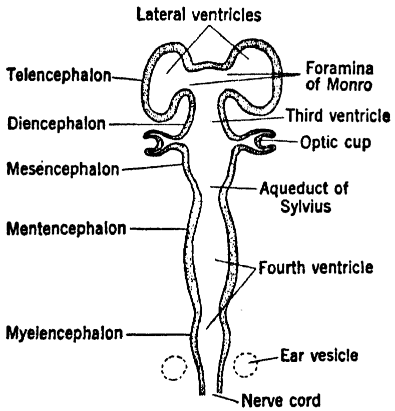


Fig. 360. Diagram of a frontal section of the brain showing its cavities. (Redrawn from Walter, *Biology of the Vertebrates*, by permission of The Macmillan Company, publishers.)

Still later the forebrain and the hindbrain become further subdivided, resulting in the formation of the type of brain characteristic of all vertebrates above the cyclostomes and consisting of five parts. The anterior portion is the telencephalon, or cerebrum. The walls of this region often become greatly expanded dorsally and laterally, forming the large cerebral hemispheres. The cavities within the cerebrum are known as the lateral, or the first and second, ventricles (Fig. 360). These are separated by a double membrane, the septum pellucidum. The second region, or diencephalon, remains relatively narrow. Its tubular cavity, or third ventricle, is connected to the lateral ventricles by two narrow passages, the foramina of Monro. The third region remains the middle part of the brain and is still known as the mesencephalon. Its dorsal wall gives rise to the optic lobes. The fourth region, or metencephalon, is a large and important part in the higher vertebrates, particularly in the mammals. It consists of the dorsal cerebellum and the ventral pons, a transverse bridge of fibers connecting the two sides of the cerebellum. The fifth and last region, the myelencephalon, or medulla oblongata, is a cone-shaped region which gradually narrows posteriorly and is continuous with the nerve cord. The cavities of the original hindbrain (metencephalon and myelencephalon) together constitute the fourth ventricle. This is connected anteriorly with the third ventricle by way of the narrow cavity of the mesencephalon, which is known as the aqueduct of Sylvius, or the iter. Posteriorly the fourth ventricle is directly continuous with the central canal of the nerve cord.

Comparative anatomy. Although the brain of the adult vertebrate of all classes (at least above the cyclostomes) is of the fundamental plan described above, much variation in general shape and details of structure appears in the different types. These differences, which are characteristic of the classes, are the result of various differential principles of growth which are illustrated in the various regions of the brain. Among the types of growth especially important in this connection may be mentioned the following: evagination, invagination, unequal thickening or "thinning" of walls, and flexures, or bendings. Evagination and invagination as mechanical principles of growth have been described before in connection with the development of numerous other organs. It will be sufficient, therefore, to say at this point that many parts of the vertebrate brain are developed either as evaginations or invaginations of the walls of a tubular cord.

In many regions of the brain the dorsal or lateral walls may become greatly thickened as compared with adjacent areas, as a result of a greater growth of cells. Conversely, other portions may fail to grow as rapidly and therefore may retain their original thinness. The roof of the cerebral hemispheres in mammals is an example of a great increase in thickness of the walls, while the roofs of the diencephalon and myelencephalon remain very thin throughout life. These thin-walled areas are supplied with networks of capillaries through which the inside of the brain receives its blood supply.

Flexures (Fig. 361), or bendings of the brain upon its long axis, take place during the development of the brain in vertebrates generally. The first of these, the parietal flexure, occurs very early in embryonic life. It is a ventral bending of the prosencephalon. The second flexure is a dorsal bending of the brain anterior to the pons, and is, therefore, known as the pontine flexure. The third, which occurs at the junction of the brain and cord, is the cervical flexure. The entire brain undergoes a second ventral bending in this region.

In the lower vertebrates such as the fishes and amphibians, there is a tendency for the brain to straighten out again. As a result, the brain of these two classes is relatively long and narrow. In the higher vertebrates the flexures are retained, making possible the development of a large brain within the limits of a more or less spherical cranial cavity.

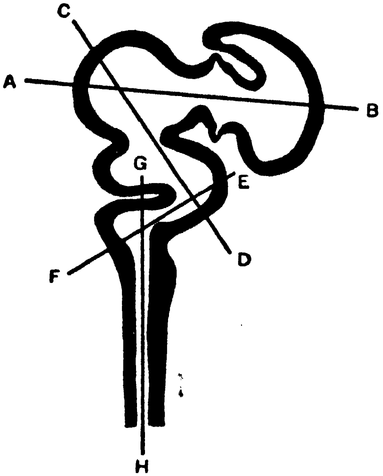


Fig. 361. Diagram illustrating the flexures of the brain. Angle between axes A–B and C–D = parietal flexure; angle between axes C–D and E–F = pontine flexure; angle between E–F and G–H = cervical flexure. (From Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

Cyclostomes. The brain of the cyclostomes is of the primitive type (Fig. 362), consisting chiefly of prosencephalon, mesencephalon, and metencephalon. The prosencephalon is composed mainly of olfactory lobes, the cerebrum being relatively small. Other sensory areas, such as the optic lobes, are also well developed. The cerebellum is little more than a transverse band of fibers anterior to the medulla. There are two small pineal bodies on the roof of the brain and the pituitary body (hypophysis) is attached to the ventral surface by an infundibulum.

Fishes. In the different fishes there is much variation in the shape of the brain. In the elasmobranchs (Fig. 363), the brain is characterized by the great development of the olfactory lobes, the cerebellum, and the medulla oblongata. The cerebral hemispheres are small and indefinitely marked off from the olfactory lobes. Two large olfactory tracts extend diagonally forward from the olfactory lobes. A stalked epiphysis develops from the diencephalon dorsally and may extend as far as the roof of the chondrocranium. The cerebellum is greatly enlarged and may extend over the posterior portions of the optic lobes, which are also extensive. Large restiform bodies of the medulla are present at the sides of the cerebellum.

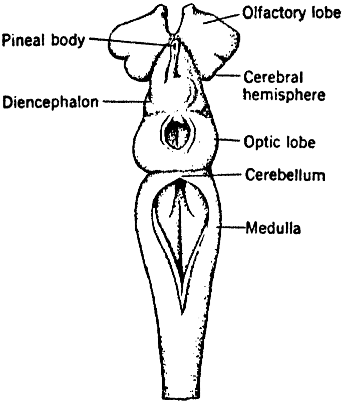


Fig. 362. The brain of a cyclostome, *Petromyzon*, dorsal view. (From Newman, *The Phylum Chordata*, after Parker and Haswell, by permission of The Macmillan Company, publishers.)

In the teleost fishes (Fig. 364), the optic lobes reach their highest stage of development. The cerebellum is often small compared to that of the elasmobranchs, growing backward over the medulla.

The brain of the lungfishes represents an advance over the other fishes and in some respects foreshadows that of the amphibians. The cerebellum is very small. The olfactory stalks have disappeared. The cerebral hemispheres are more definite and show a thickening of the dorsal walls (pallium), which now contain nerve tissue.

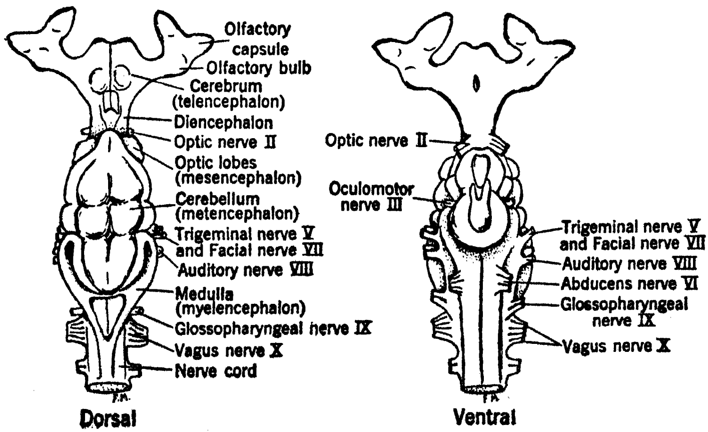


Fig. 363. The brain of an elasmobranch.

Amphibians. The amphibian brain (Fig. 365) is somewhat similar to that of the elasmobranch fishes in general appearance. The olfactory lobes are large, and the cerebral hemispheres are more definitely separated from them. The pallium is somewhat thicker than in the Dipnoi and contains more numerous neurons. The optic lobes are of large size and are more laterally located. The cerebellum is very small,

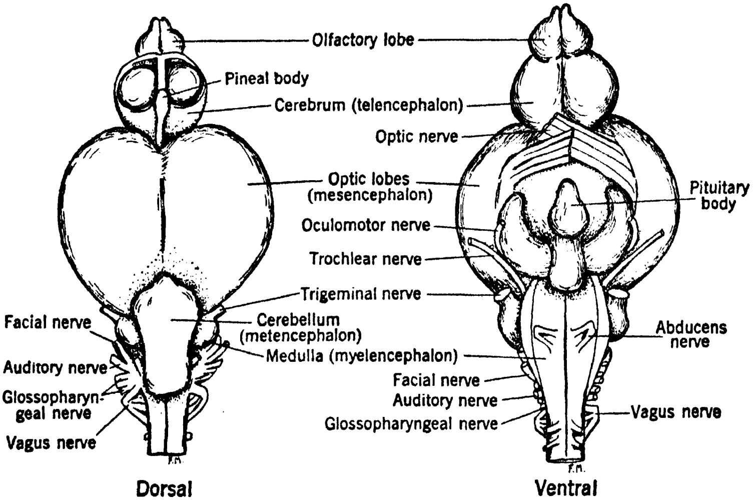


Fig. 364. The brain of a teleost.

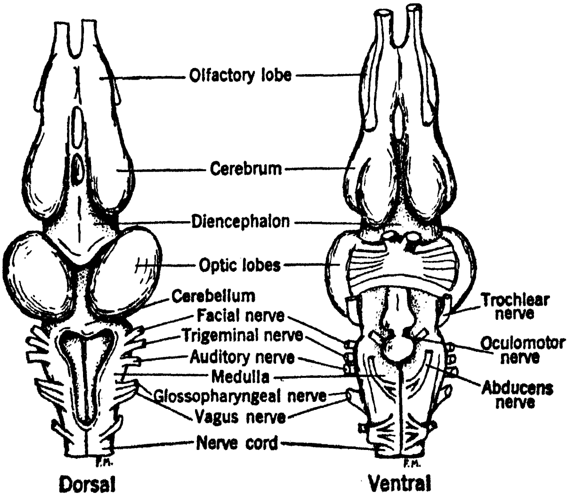


Fig. 365. The brain of the frog.

consisting of a narrow, transverse band just anterior to the medulla.

Reptiles. The brain of reptiles (Fig. 366) shows a noteworthy advance over that of the preceding classes, especially in the greater development of the pallium. The olfactory lobes are generally smaller than in the lower vertebrates.

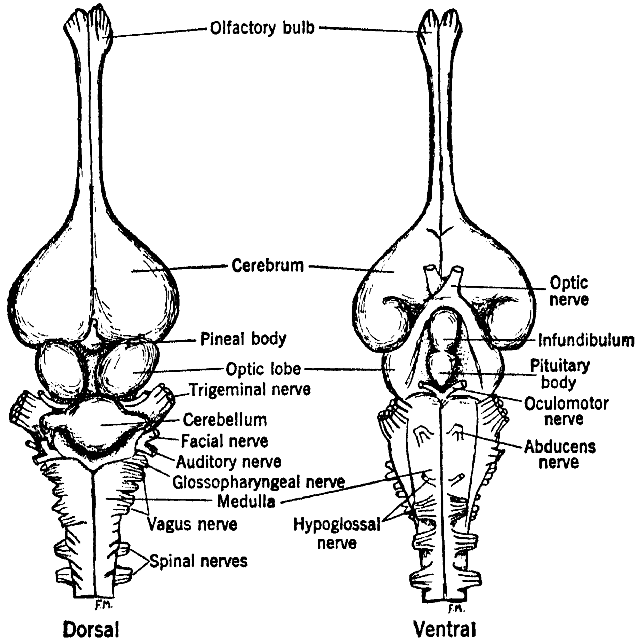


Fig. 366. The brain of the alligator.

The region of the diencephalon includes several organs of special interest, such as the large hypophysis and the parietal organ. The former structure is differentiated into an anterior and a posterior lobe, while the parietal organ extends to the dorsal surface of the skull. In *Sphenodon* and several other reptiles it forms a well developed eye, the pineal or, more properly, the parietal eye. The optic lobes are somewhat reduced, while the cerebellum has increased in size and importance.

Birds. The avian brain (Fig. 367) has been referred to as an "eye brain" because of the presence of large optic lobes. The olfactory lobes are correspondingly reduced. The cerebrum has increased greatly in size and extent, but not in the thickness of the pallium. The hemispheres have grown posteriorly, thereby crowding the large optic lobes into a more lateral position. The cerebellum has grown forward almost to meet the cerebrum and to cover the diencephalon dorsally. The median dorsal surface of the cerebellum, which bears a series of transverse grooves, is known as the vermis,

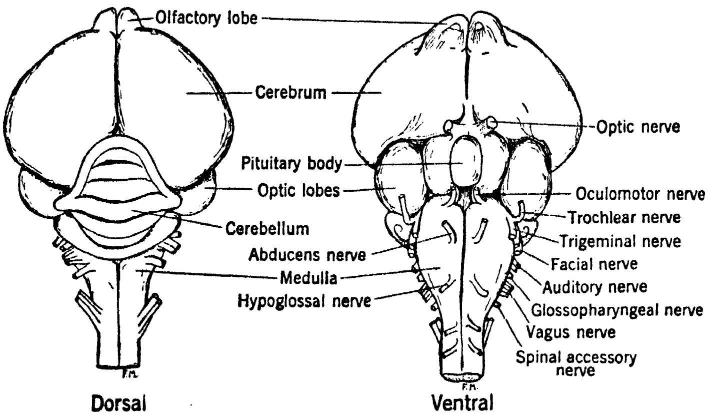


Fig. 367. The brain of the pigeon.

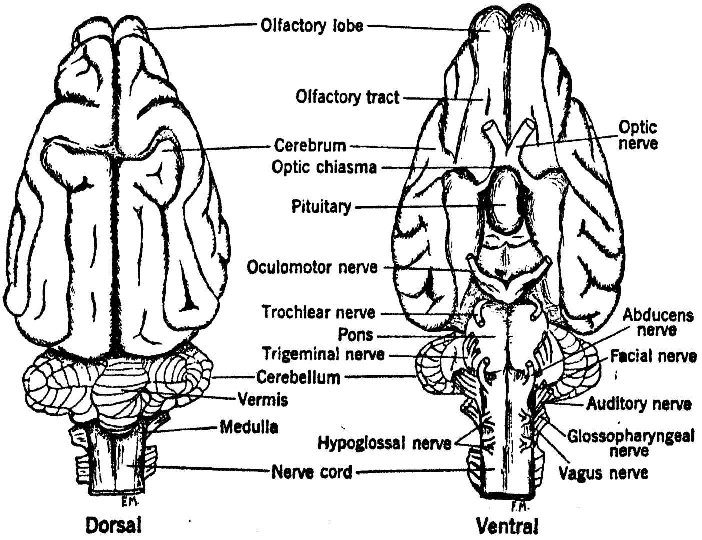


Fig. 368. The brain of a mammal.

because of its resemblance to a segmented worm. The two lateral regions are the flocculi.

Mammals. The brain of mammals (Fig. 368) is relatively much larger than that of the preceding classes. This is due chiefly to the great enlargement of the cerebrum and cerebellum, particularly of the cerebral cortex. The diencephalon is small and is covered over dorsally by the cerebral hemispheres. The hypophysis is a well-developed endocrine gland. The epiphysis is small and has also probably become an organ of glandular rather than sensory function. The optic lobes are relatively small and are covered by the cerebral hemispheres. The dorsal surface of the lobes forms the so-called corpora quadrigemina. The cerebellum is well developed, comprising, in addition to the vermis, well-developed lateral hemispheres. The pons, a transverse band of fibers in the ventral region of the metencephalon, is distinctive. The short medulla is largely covered over by the cerebellum (Fig. 370).

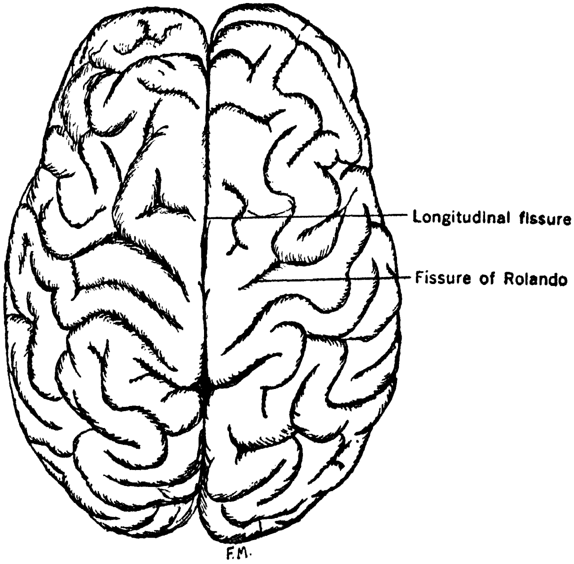


Fig. 369. The brain of man, dorsal view.

The surface of the cerebrum is relatively smooth in lower mammals but in the higher forms is characterized by numerous grooves extending in various directions, leaving raised portions or convolutions between them (Fig. 369). The shallow grooves are known as sulci; the deeper and more extensive ones, as fissures. The convolutions are also called gyri.

Internally (Fig. 372 C) the mammalian brain shows many distinctive features. Among these may be mentioned particularly the various commissural tracts (transverse fibers) which connect the two sides. The most important of these is the corpus callosum, a large body of such fibers, connecting the hemispheres of the cerebrum. The cavity of the mesencephalon as mentioned above is a narrow tube, the iter, or aqueduct of Sylvius, connecting the third and fourth ventricles.

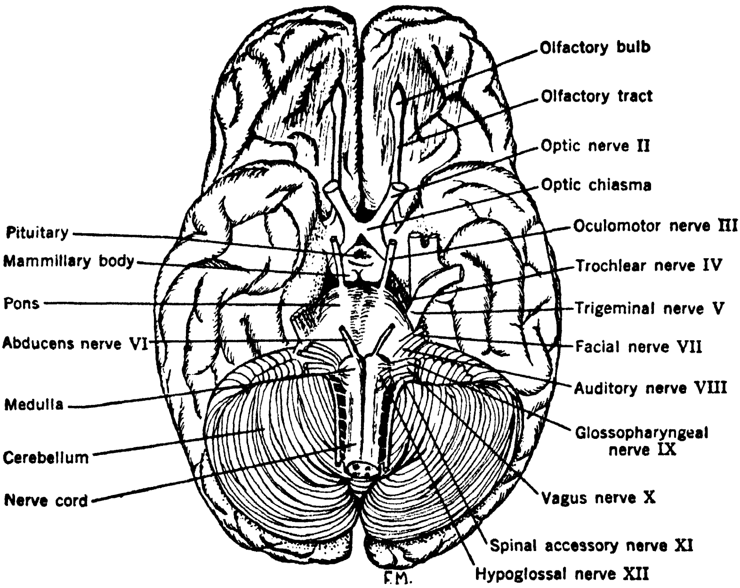


Fig. 370. The brain of man, ventral view.

The Peripheral Nervous System

This part of the nervous system includes the cranial and spinal nerves. The cranial nerves are those which communicate with the brain directly, while the spinal nerves connect with the nerve cord (Fig. 373). The sympathetic nerves and ganglia are connected with the other nerves by small connecting branches, the rami communicantes.

The spinal nerves. These are connected to the nerve cord by dorsal and ventral roots (Fig. 374). Within the cord, as described above, these roots are continuous with the dorsal and ventral cornua of the gray matter of the cord. Distally, the two roots pass laterally through the intervertebral foramina, thereby retaining their primitive segmental arrangement. Associated with the dorsal root is a group of cell bodies of neurons, the dorsal ganglion. Somewhat distal to the dorsal ganglion, the roots unite to form a combined nerve which again branches still more distally to form dorsal and ventral nerves. Dorsal and ventral nerves and the combined nerve contain both sensory and motor fibers. The motor neurons may be either visceral or somatic. The visceral components are on their way to the autonomic ganglia and through them to such structures as blood vessels and glands which are located in outlying regions of the body. The dorsal roots contain only sensory neurons whose cell bodies are located in the dorsal ganglia. The ventral roots, on the other hand, consist of motor neurons, whose cell bodies are located in the gray matter of the cord. Since the combined nerve

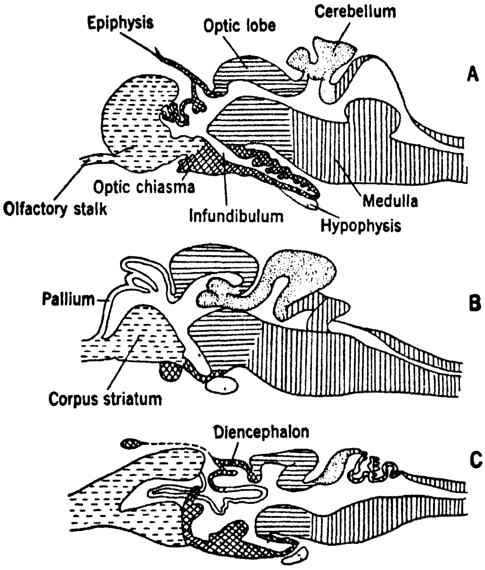


Fig. 371. Diagrams of sagittal sections of the brain. A, elasmobranch; B, teleost; C, amphibian. (Redrawn from Walter, *Biology of the Vertebrates*, after Edinger, by permission of The Macmillan Company, publishers.)

receives the ramus communicans from the corresponding sympathetic ganglion, it contains all four kinds of neurons; somatic sensory from the outlying parts of the body on their way to the cord by way of the dorsal root and ganglion; somatic motor returning from the cord to outlying organs, such as the voluntary muscles in general; visceral sensory from the viscera on their way to the cord, as in the case of the somatic sensory; and finally, visceral motor, which may be of two kinds, preganglionic from the ventral root to the ramus and thence to the sympathetic ganglion, and postganglionic from the ganglion to a superficially located blood vessel or gland. Postganglionic neurons distributed to the viscera in general reach their destination by way of the main sympathetic trunk and its branches.

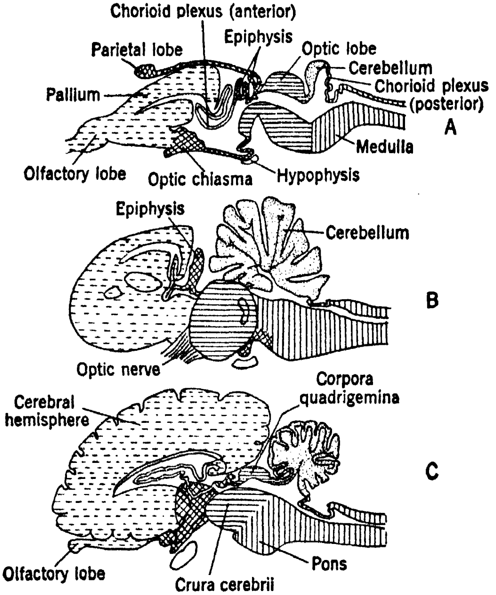


Fig. 372. Diagrams of sagittal sections of the brain. A, reptile; B, bird; C, mammal. (Redrawn from Walter, *Biology of the Vertebrates*, after Edinger, by permission of The Macmillan Company, publishers.)

The spinal nerves as they issue between the vertebrae are given corresponding names. The number of spinal nerves in a given animal depends upon the number of vertebrae. In man, for example (Fig. 373), there are eight cervical, twelve thoracic, five lumbar, five sacral, and one coccygeal nerve. The first cervical nerve issues between the skull and the first cervical vertebrae, giving eight nerves to only seven vertebrae in this region.

The spinal nerves in the region of the limbs divide, unite with one another, and again divide to form intricate networks known as plexuses. These are the branchial and the lumbosacral plexuses.

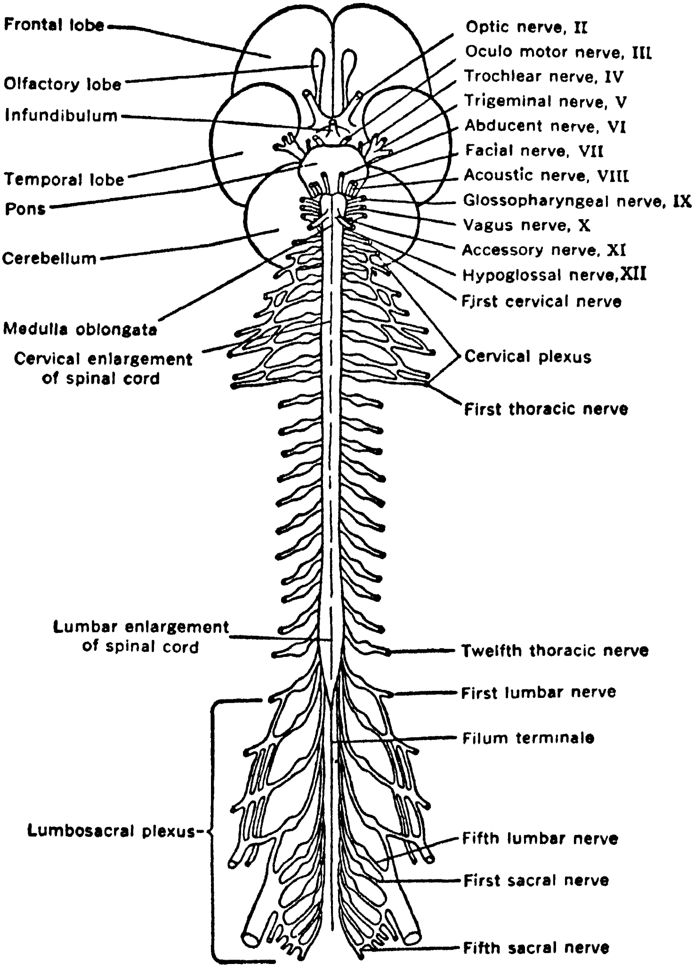


Fig. 373. The central nervous system of man showing the origin of the cranial and spinal nerves. (From Mavor, *General Biology*, by permission of The Macmillan Company, publishers.)

In man the last four cervical and the first thoracic nerves enter the brachial plexus. Distal to the plexus several nerves continue into the arm, the largest of which are the ulnar, radial, and median nerves. All the lumbar, sacral, and coccygeal nerves enter into the formation of the lumbosacral plexus. Distally two large nerves, the femoral and sciatic, emerge and continue with their branches into the hind leg and foot.

THE CRANIAL NERVES. These are nerves which arise from some part of the brain, and in general they supply the sense organs and other important structures of the head and neck. They are embryologically similar to the spinal nerves in their segmental arrangement and in their relation to the brain. In the adult, however, because of the degree of cephalization characteristic of the vertebrates, they lose much of their original similarity to the spinal nerves. Those innervating the sense organs are entirely sensory, those supplying the muscles of the eyeball are entirely motor, while the others are mixed nerves; that is, both sensory and motor.

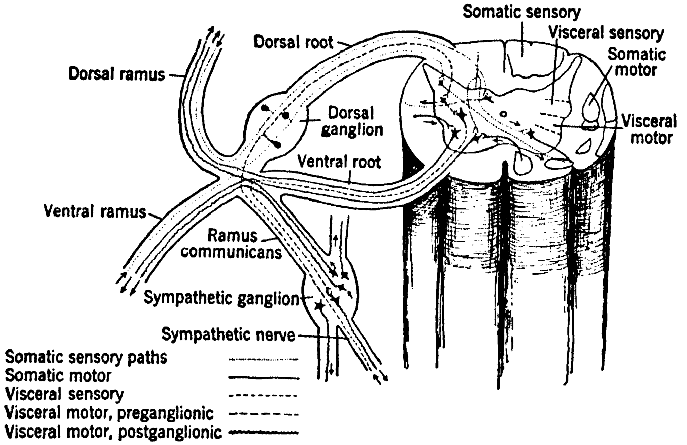


Fig. 374. Diagram showing the parts of a typical spinal nerve, and their relation to the nerve cord. (Redrawn from Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

For many years it has been considered and so stated in textbooks that there are eight cranial nerves in the cyclostomes, ten in the fishes and amphibians, and twelve in the reptiles, birds, and mammals. These were numbered with Roman numbers, beginning with the most anterior, and also given names with reference to the structures which they

Number	*Name*	*Superficial Origin*	*General Function*	*Distribution*
0	Terminal	Telencephalon	Sensory	Olfactory membranes
I	Olfactory	Telencephalon (Olfactory Bulb)	Sensory	Olfactory membranes
II	Optic	Diencephalon	Sensory	Retina of the eye
III	Oculomotor	Mesencephalon	Motor	Muscles of the eye (inferior oblique; superior, inferior, and internal rectus)
IV	Trochlear	Mesencephalon	Motor	Muscle of the eye (superior oblique)
V	Trigeminal	Metencephalon	Sensory and Motor	Jaws, skin, teeth, tongue, and muscles of mastication
VI	Abducens	Myelencephalon	Motor	Muscle of the eye (external rectus)
VII	Facial	Myelencephalon	Sensory and Motor	Anterior taste buds, salivary glands and muscles of the face
VIII	Auditory	Myelencephalon	Sensory	Semicircular canals and the organ of Corti
IX	Glosso-pharyngeal	Myelencephalon	Sensory and Motor	Pharynx, tongue, and parotid gland
X	Vagus	Myelencephalon	Sensory and Motor	External ear, pharynx, larynx, trachea, esophagus, and the viscera of thorax and abdomen, via sympathetic ganglia
XI	Spinal accessory	Myelencephalon	Motor	Voluntary muscles of larynx and trachea. Trapezius and sternocleidomastoid muscles
XII	Hypoglossal	Myelencephalon	Motor	The muscles of the tongue

innervated. Quite recently, and long after this terminology had been well established, an additional nerve, anterior to the others, was discovered in the African lungfish (*Protopterus*). This is known as the terminal nerve and is referred to as N. O. to avoid interfering with the original numbering system. It is a large nerve in the elasmobranch fishes and has been shown to be present in all vertebrates above them, with the exception of the birds. It is now thought to be associated with the autonomic system.

The table on page 385 summarizes the origin, function, and distribution of the thirteen cranial nerves of the higher vertebrates.

The Autonomic System

The autonomic division of the nervous system is that part which is concerned with the activities of the smooth muscles of the viscera, of most glands, and of other organs not consciously controlled by the individual. This division of the nervous system, like the voluntary, consists of nerves, ganglia, and plexuses. It includes both inhibiting and accelerating fibers. So many different names have been applied to this division of the nervous system that considerable confusion has arisen. It has been studied particularly in the mammals where it is especially well developed. According to a recent classification it may be divided, in the members of this class, into the parasympathetic, the sympathetic, and the enteric systems. The first of these is also often called the craniosacral division; while the sympathetic system is often referred to as the thoracolumbar.

The parasympathetic system includes all fibers which arise from the midbrain, the medulla, and the sacral portion of the nerve cord. These fibers convey a wide variety of impulses including motor impulses to the muscles of the iris and to the smooth muscles of various parts of the digestive tract; secretory impulses to the stomach, liver, and pancreas; inhibitory impulses to the heart; and motor, vasodilator, or inhibitory impulses to the posterior parts of the alimentary canal and to the genital organs.

The sympathetic system includes centers in the different regions of the cord (except sacral) and the preganglionic fibers which arise from them; the chains of sympathetic ganglia and the main sympathetic trunks; and the various plexuses which arise from the ganglia.

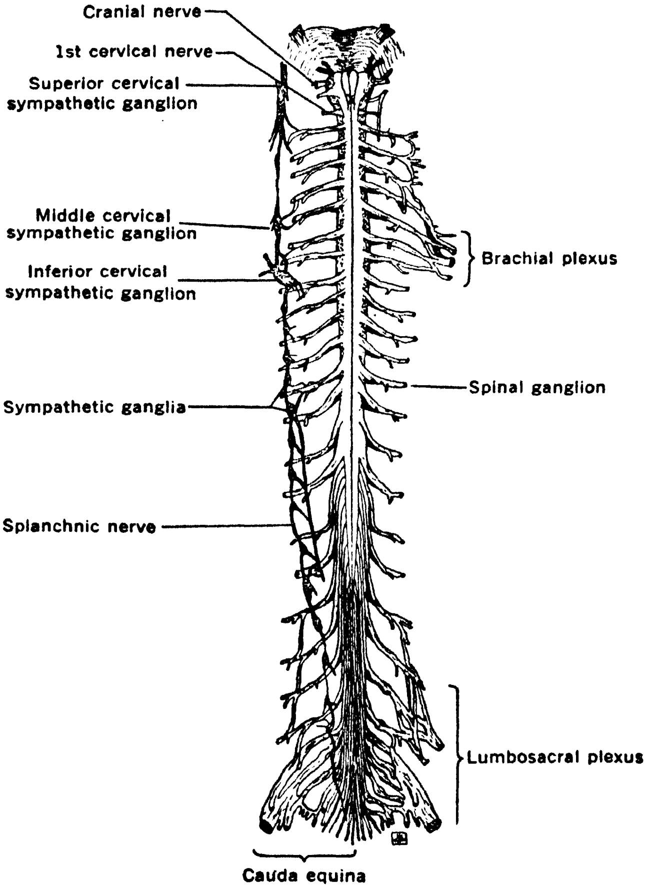


Fig. 375. The spinal cord of man, showing the plexi, the cauda equina, and on one side, the sympathetic nerve chain. (From Walter, *Biology of the Vertebrates*, after Rauber, by permission of The Macmillan Company, publishers.)

In a typical vertebrate there are two parallel chains of ganglia extending longitudinally (Fig. 375) just ventral to the centra. These ganglia are connected with one another longitudinally and sometimes transversely by nerves, and with the adjacent spinal nerves by the rami communicantes. Extending from these chains of ganglia are nerves which lead to the different organs of the body. Along the route these nerves pass through various relaying centers either in the form of ganglia or plexuses. These plexuses serve to increase the number of possible pathways leading to the viscera. Among the largest of these plexuses may be mentioned the aortic, cardiac, solar, and hypogastric.

The enteric division includes a number of plexuses in the walls of the digestive tube. Some of these are between the smooth muscle coats, while others are located in the submucosa.

Nerve activity involving the autonomic system might take the following course — from the receptor by way of a sensory neuron, which would pass through the sympathetic ganglion, then by way of a ramus communicans to the dorsal ganglion of a spinal nerve, and thence into the cord. The motor pathway, that is, from the cord to the effector, differs from that of the voluntary fibers of a spinal nerve in that there are two orders of neurons involved; preganglionic and postganglionic neurons. The preganglionic carry the impulse from the spinal cord in which they arise to a ganglion of the main autonomic trunk or to one of the more distal ganglia. The postganglionic relay the message from this point to the effector located in some organ.

It will be seen from the above description and from a study of Fig. 375 that the autonomic nervous system is not a distinct series of nerves; rather, it is closely associated with other parts of the nervous system. It has been stated that the spinal nerves, in both their dorsal and ventral roots, carry both somatic and visceral fibers. Some of the cranial nerves, particularly the vagus, also carry many visceral fibers from the brain to involuntary muscles or to glands. Many of the activities initiated by the autonomic system are controlled (accelerated or inhibited) by these visceral fibers of the vagus nerve.

SUMMARY

The nervous system is one of the great coordinating mechanisms of the body, playing an important part in regulating the activities of the other systems. The structural units of the system are the neurons or nerve cells. These consist of a cell body or cyton and various threadlike processes of cytoplasm. The nerve cells are specialized for the conducting of impulses from the sense organs to the brain and from the brain to a responding organ such as a muscle or gland. The functional unit of the nervous system is known as a reflex arc. This usually consists of a sense organ, a sensory neuron, an association neuron, a motor neuron, and an effector (muscle or gland).

The vertebrate nervous system is of ectodermal origin, developing in the median dorsal region by a process of invagination. The anterior portion of the tube thus formed is modified to form the brain, the remainder is the nerve cord.

The system may be divided into three parts, the central, the peripheral, and the autonomic. The former contains the brain and the nerve cord, the peripheral includes the cranial and spinal nerves, while the latter includes those nerves associated with involuntary visceral activities.

The nerve cord retains its typical tubular character but is subject to much variation in the different classes. In general it tapers gradually from the anterior toward the posterior end, except for the two enlargements in the region of the appendages. The shape of the cord as seen in cross section is more or less circular with median dorsal and ventral grooves. The inner gray matter, consisting largely of bodies of neurons, is definitely separated from the outer white matter, in the higher vertebrates. The white matter of the cord contains ascending (sensory) and descending (motor) columns of nerve fibers. In mammals the gray matter is in the form of a letter H, with the central canal in the crossbar and dorsal and ventral nerve roots continuous with the lateral portions. The nerve cord is covered with several enveloping membranes or meninges with lymph-filled spaces between them.

The brain first appears as an expansion of the anterior end of the cord. Two transverse constrictions divide this into three regions, the forebrain, the midbrain, and the hindbrain. The forebrain and hindbrain are each subsequently divided into two regions, giving a brain consisting of five parts or vesicles, each of which contains a tubular canal or an expanded cavity, or ventricle. Later on, by various kinds of growth in definite regions, such as invagination, evagination, thickening or thinning of walls, and bendings, the adult brain characteristic of the different classes is formed.

The brain of the cyclostomes is of the primitive type consisting of three parts. The sensory areas are relatively large while the cerebrum is small. In the elasmobranchs the olfactory lobes, optic lobes, cerebellum, and medulla are large, while in the teleost fishes the optic lobes are most prominent.

The amphibian brain is similar to that of the elasmobranchs except for a clearer distinction between the olfactory lobes and the cerebrum. In the reptiles an advance is seen in the greater development of the roof of the cerebrum, and of such structures as the hypophysis and pineal body.

The bird brain is characterized by the large optic lobes and the increase in size of the cerebrum and cerebellum. The brain of mammals is relatively larger than that of any other class. This is due largely to the great development of the cerebrum and cerebellum. The numerous convolutions on the surface of the cerebrum and the presence of a corpus callosum are distinctive features.

The peripheral nervous system includes the cranial and spinal nerves. The cranial nerves are those which lead directly from the brain. Aside from the terminal nerve there are eight pairs in the cyclostomes, ten pairs in fishes and amphibians, and twelve in the higher vertebrates. The spinal nerves are those leading to and from the nerve cord.

The autonomic portion of the system is concerned with the involuntary activities of the various organs. This consists of series of ganglia and nerves which are connected to the spinal nerves by means of the rami communicantes.

XV. *The Sense Organs*

In the discussion of the nervous system in the preceding chapter, mention was made of the sense organs, which serve as receptors which initiate the activity of the nervous system. We now turn to a more complete consideration of these sense organs, their location, structure, and role in the life of the vertebrates. We have seen that the nervous system serves to regulate and control the various activities of the organs of the body, in response to both external and internal stimuli, through the specialization of the neurons for conductivity. The sense organs are specialized cells which receive the original stimulus and pass the resulting impulse on to a sensory transmitter. The sense organs, whether simple or complex, are specialized along the line of sensitivity to a change in environment, in other words, to a given stimulus.

The simplest kind of receptor consists of a sensory neuron whose many branches form a network between the epidermal cells of the skin. The functional unit of any definite sense organ may be considered to be a specialized epithelial cell, which is in contact with the ending of a sensory neuron. From this simple condition, complexity and greater efficiency may be obtained, first by the grouping together of several of these simple cells to form a larger sensory area, and secondly by the addition of other tissues which serve to protect the sensory cells or to direct, control, or modify the stimulus. Many of the simple sense organs remain in the skin, more frequently in the deeper regions, or dermis. These are concerned with the perception of such qualities as heat, cold, touch, pressure, etc. Other sense organs of a simple nature are located internally or in the viscera; for example, those in various parts of the digestive system which are associated with such sensations as hunger and thirst. The more complex sense organs are those concerned with the special senses such as tasting, smelling, hearing, and seeing. The organs concerned are, respectively, taste buds, the olfactory membrane, the ear, and the eye. Taste and smell are sensations caused by stimuli that are chemical in nature, while hearing and seeing are the results of physical stimuli.

It is not necessarily safe to assume that the lower vertebrates respond to these different stimuli in the same way that man does, even though they possess similar structures. The simple sense organs stimulated by contact (touch, pressure, etc.) apparently were developed in the invertebrates and have been carried over into vertebrate history. Sensitiveness to taste and smell also is apparently a characteristic of all vertebrates, as well as of many lower animals. Sight was also an early development and its organ, the eye, is a very highly developed and efficient structure in most vertebrates above the cyclostomes. The sense of equilibrium in invertebrates has its own system of organs, the statocysts. In the fishes the ear is concerned, very largely, with this sense, that of hearing having been added as an adaptation for terrestrial life. Some recent investigations, however, point to the conclusion that some fishes are able to distinguish certain sounds. Closely associated with the ear are the lateral line and related organs, characteristic of the aquatic classes of vertebrates, which are sensitive to stimuli caused by changes in pressure or currents, in a liquid medium.

SENSORY CORPUSCLES

Among the simpler of the sense organs are the so-called tactile corpuscles, which are found quite generally distributed in the mammalian integument and to a lesser degree in the skin of some of the lower classes. These are typically oval or elliptical groups of sensory cells surrounding the endings of a sensory neuron and in turn surrounded and protected by a covering of connective tissue cells (Fig. 376). In Merkel's corpuscles the branching dendrites of the neuron form cups under the epithelial cells. Meissner's corpuscle is made up of an oval mass of epithelial cells, among which the sensory nerve endings are spirally wound. In the end bulbs of Krause, the nerve endings resemble a capillary glomerulus within a spherical capsule of connective tissue cells. Grandry's corpuscles, which are found only in the beaks of certain birds, consist of two enlarged sensory cells with the nerve ending between them. Based on a similar plan are Herbst's corpuscles, also found only in birds. These consist of two rows of cells with the nerve ending between them. Both of these types are in capsules of connective tissue.

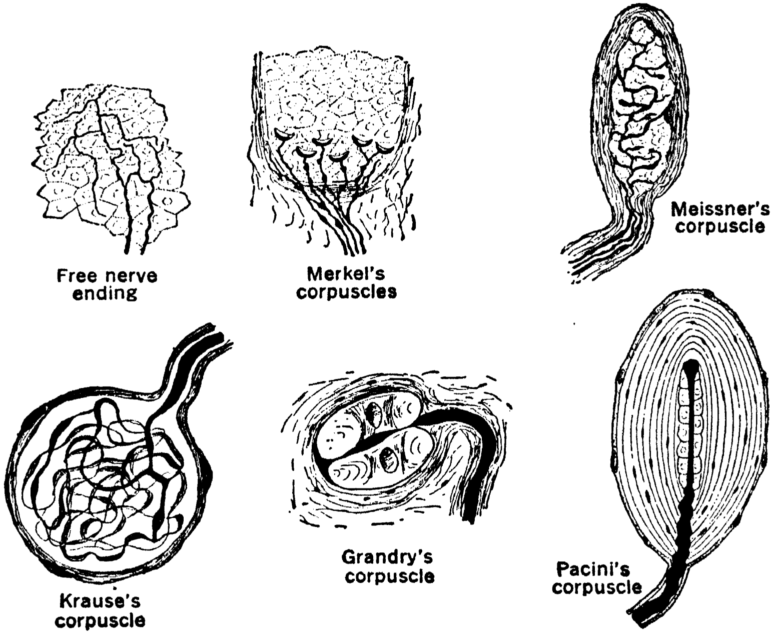


Fig. 376. Diagrams of sensory nerve endings. (From Wilder, *The History of the Human Body*, by permission of Henry Holt and Company.)

One of the most complicated of the sense organs of this type is the Pacinian corpuscle. In this corpuscle the sensory cells are in rows surrounding the nerve ending and are in turn surrounded by several layers of connective tissue resembling the lamellae of an onion. These are found not only in the deeper layers of the skin, but also in tendons and joints, in the mesenteries, in the pleural and peritoneal lining of the body cavities, and within the interstitial tissue in the pancreas.

PRESSURE OR CURRENT RECEPTORS

The aquatic vertebrates are provided with several kinds of sense organs which are concerned with registering changes of pressure or direction of currents. Fundamentally, these organs consist of small clusters of cells, provided with sensory hairs and associated with a sensory branch of one of the cranial nerves. Typically each of these units, which have

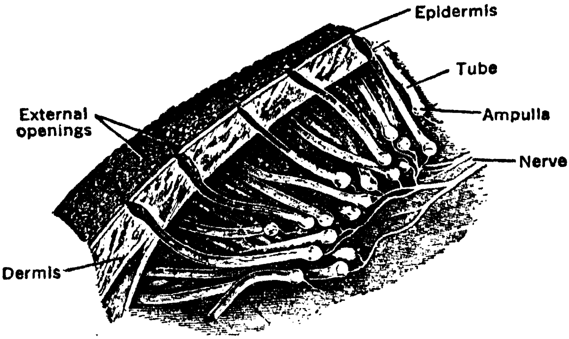


Fig. 377. Section of the snout of *Scyllium* showing ampullary tubes. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, after Gegenbaur, by permission of The Macmillan Company, publishers.)

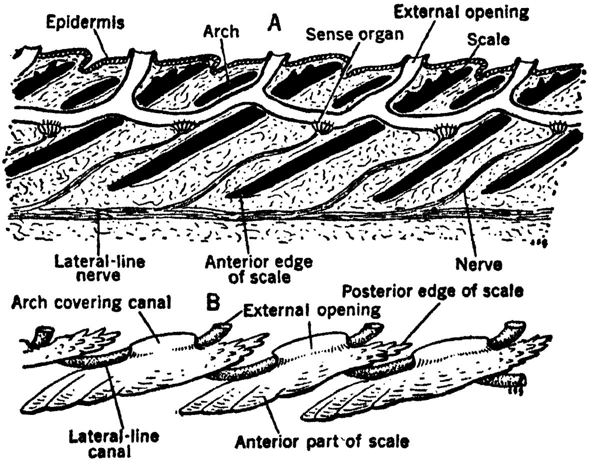


Fig. 378. Diagrams showing the relation of the lateral line canals to the scales of the perch. A, longitudinal section; B, the scales and the canal seen from the side. (From Goodrich, *Studies on the Structure and Development of Vertebrates*, by permission of The Macmillan Company, publishers.)

been called neuromasts, opens directly to the external surface by means of a pore. Some of them may be located at the bottom of deep pits which are filled with mucus, through which the stimulus must pass to reach the sensory hair.

The ampullae of Lorenzini (Fig. 377), found only in elasmobranch fishes, are large and highly modified organs of this character. They lie deeply buried below the surface in a rounded cavity, which is filled with mucus. In the head of many other fishes are several definite rows of similar organs located in shallow grooves at the bottom of which the pores open.

The lateral line organs (Fig. 378), so characteristic of fishes in general, are made up of a linear series of these simple organs. These are usually grouped in a single line which extends the length of the body in a groove or in a canal, between the dorsal and ventral divisions of the body muscles. The pores from the individual organs of the series may open through the scales or between them. The Lateral Nerves, which are branches of the Vagus (N. X), supply these organs. The lateral line organs, in addition to the functions mentioned above, also respond to sounds of low vibrations.

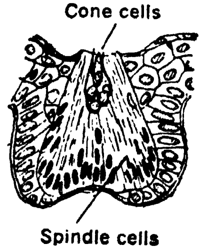


Fig. 379. Section through a sense organ of the lateral line of a newt, *Triturus*. (From Walter, *Biology of the Vertebrates*, after Kingsbury, by permission of The Macmillan Company, publishers.)

ORGANS OF TASTE

The sense of taste is limited to distinguishing such qualities as sweet, bitter, sour, or salty, all of which are chemical in nature. The unit of function is a taste bud. In fishes these may be quite widely scattered throughout the skin on the sides of the body, where they serve to indicate the presence of food. In higher vertebrates they are confined to the mouth cavity and chiefly to the lips and tongue. In the tongue they are closely associated with the various kinds of papillae which characterize the surface of that organ.

A taste bud (Fig. 380) is a spherical body consisting of a number of spindle-shaped sensory cells and somewhat similar but larger supporting cells. The buds lie just below the surface of the tongue, with the free ends of the sensory cells, which are provided with delicate flagellae, projecting towards a pore formed between the supporting cells. The inner ends of the receptor cells make contact with the dendrites of branches of the Glossopharyngeal (N. IX), or with a small branch of the Facial (N. VII).

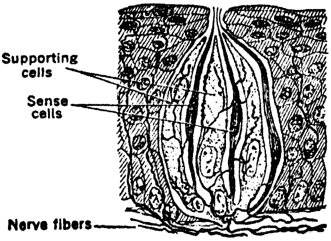


Fig. 380. Diagram of a taste bud in epithelium of tongue. (From Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

THE ORGAN OF SMELL

The organ of smell is concerned with distinguishing the various kinds of odors given off from different bodies. The sense of smell, therefore, resembles that of taste in being chemical in nature, the odors being brought to the organ either through the medium of water or of air. The receptor cells are located in the olfactory (epithelial) membranes (Fig. 381), which line parts of the nasal cavities. The olfactory cells resemble nerve cells in having a cell body containing a nucleus, an axon, and a dendrite. The free ends (dendrites), in the mammals, are provided with fine cilia, while the axons pass through openings in the cribriform plate of the ethmoid bone and lead directly into the brain itself (olfactory lobe, or bulb). These receptor cells, therefore, resemble neurons in their function as well as structure. The olfactory nerve properly is a combination of all the axons leading from these cells to the olfactory bulb.

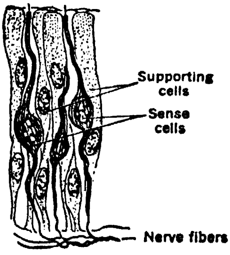


Fig. 381. Cells of olfactory epithelium from human nose. (From Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

In typical aquatic forms the olfactory membranes line blind cavities within the head, which are in communication with the external surface by means of the external nares. In such forms the nasal cavities are concerned with the olfactory sense only. In terrestrial (air-breathing) vertebrates the membranes are on the walls of nasal cavities which also communicate internally with the pharynx, since these cavities serve also as the respiratory pathways.

In the cyclostomes a single median nostril (external naris) is present. In the lampreys (*Petromyzon*) this leads into a blind sac, as in typical aquatic vertebrates. In the hagfishes, the nasal cavities continue posteriorly to communicate with the pharynx, as in air-breathing forms. This difference is associated with their parasitic habits. When the mouth is employed in feeding on the body of their prey, it cannot be used as an inlet for the respiratory medium (water). At such times the nasal passage serves as the respiratory pathway, as it does in terrestrial forms. In the lampreys, the gill slits serve both as incurrent and excurrent respiratory routes during feeding.

In the typical fish the nasal cavities do not communicate with the pharynx; so only external nares are present. In many forms two external openings are present on each side of the head. In the lungfish internal nares are present. In this group, as in the amphibians, they open into the anterior region of the mouth cavity. In the reptiles with the development of a hard palate, formed by the medial growth of the maxillary and palatine bones, these internal openings are carried back into the pharynx, the posterior part of the mouth cavity.

The efficiency of the olfactory membranes is roughly proportional to the area of their surfaces and their degree of moisture. Consequently, we find in the different vertebrates many provisions for increasing the surface area of the membranes and for keeping them moist. In the fishes not only does the olfactory epithelium surround the entire cavity, but also many leaflike folds project from it into the cavity. In the amphibians, also, almost the entire cavity is lined with the membrane, while in terrestrial forms it is usually confined to the dorsal walls.

In reptiles, birds, and mammals thin shelves of bone, the conchae (turbinals), develop from the bones surrounding the cavity and project into it. Both surfaces of these plates may be covered with epithelial membranes containing either olfactory or glandular (mucous) cells. These are especially well developed in the mammals (Fig. 382), particularly in the ungulates and carnivores. There are typically three series of these structures, the nasoturbinals, ethmoturbinals, and maxilloturbinals, named after the bones from which they develop. In many mammals, as in the deer, the maxillo-turbinals may be in the form of a double scroll which greatly increases the area possible within a given space.

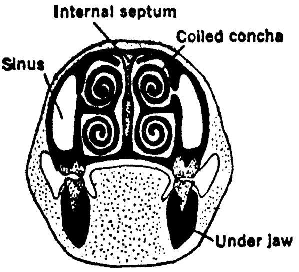


Fig. 382. Diagrammatic cross section through the nasal region of a mammalian head. (From Walter, *Biology of the Vertebrates*, after Boaz, by permission of The Macmillan Company, publishers.)

The size of the nasal cavities is further increased in many vertebrates by numerous communicating air spaces within surrounding bones. These may be in the form of definite cavities, or sinuses, such as are found in the maxillary, sphenoid, and frontal bone in many mammals, or in the form of more extensive spongy areas of bone, such as those found in the elephant skull and within the mastoid process of man.

To function effectively the olfactory membrane must be kept moist. This is accomplished, in terrestrial forms, by the activity of numerous sebaceous and mucous glands located within the nasal chambers, and also by the overflow from the lacrimal (tear) glands.

THE ORGAN OF HEARING AND EQUILIBRIUM

It was implied above that the vertebrate ear was primarily an organ concerned with the static sense (equilibrium) and that it took on the additional function of hearing when the vertebrates left the water and took up terrestrial life. For the sake of convenience and to avoid unnecessary repetition of detail, the structure of the mammalian ear will be described first. This will be followed by a consideration of the differences in this organ in the different vertebrate classes and by a description of those parts primarily concerned with equilibrium.

THE MAMMALIAN EAR. The ear of the typical mammal consists of three regions — the outer, the middle, and the inner ear (Fig. 383). The sense of hearing consists of the reception and interpretation of vibrations, or sound waves, reaching an animal through the medium (water or air) in which it lives. The inner ear contains the essential sensory receptor cells and is present in all vertebrates possessing the sense of hearing. The interpretation of these sound waves is a function of the nervous system. The outer and middle ear contain accessory structures which collect, direct, and modify these vibrations.

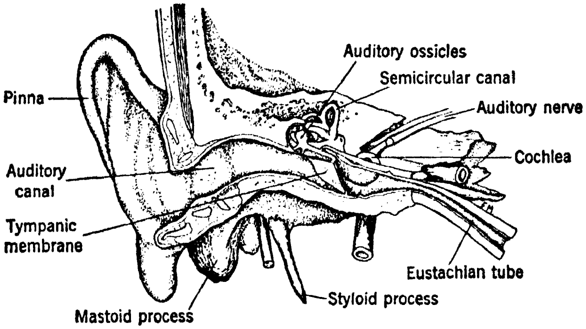


Fig. 383. Section of the human skull showing parts of the ear. (Adapted from the American-Frohse Anatomical Charts, courtesy of A. J. Nystrom and Company, Chicago.)

The outer ear. The outer ear in this class of vertebrates consists of the pinna, the external auditory aperture, and the auditory canal. The pinna is a membranous flap covered by skin and supported by cartilage which partially surrounds the ear opening. Controlled by voluntary muscles, its primary function is to collect sound waves, determine the direction from which they come, and direct them to the opening into the auditory canal. The pinnae are very much reduced in aquatic and burrowing types, while they are especially well developed in arboreal and nocturnal mammals. Muscular movement of this structure has been practically lost in man and several other mammals.

The auditory canal is a tubular passageway leading from the external opening through the temporal bone to the middle ear. In man it is approximately one inch in length. It represents the integumentary invagination which is the homologue of the spiracular cleft in elasmobranch fishes, between the first and second visceral arches. The skin lining the canal contains hairs and wax glands, both of which serve to prevent the entrance of dust, insects, or other foreign bodies.

At the inner end of the auditory canal a thin membrane, the ear drum, is stretched across the cavity. This membrane (tympanic) is supported by a bony ring, the annulus tympanicus, and separates the outer from the middle ear. The tympanic membrane represents that double layer of tissue, between the spiracular cleft and pouch of the elasmobranchs, which fails to break through to form a slit. It therefore consists of an external layer of ectoderm and an internal layer of endoderm.

The middle ear. The middle region of the ear is an irregular shaped cavity (tympanum) within the temporal bone of the skull. It is derived phylogenetically from the inner portion (pouch) of the spiracle of the primitive vertebrate. It is in communication with the spongy cavities within the mastoid process and, by means of the Eustachian tube, with the pharyngeal cavity.

Through the bone forming the inner wall of this cavity are two openings, or windows: the fenestra cochleae (round window) and fenestra vestibuli (oval window), both of which are covered by thin membranes.

Extending across the middle ear are the three auditory bones, or ossicles: the malleus, the incus, and the stapes (Fig. 384), the homologies of which have been previously mentioned (Chapter VII). They are attached to one another and held in place by muscles and ligaments. The outer of the three, the malleus, is in contact with the surface of the tympanic membrane, while the flattened end of the inner bone, the stapes, fits into the oval window and makes contact with the membrane covering it.

The inner ear. The internal portion of the ear consists of an irregular-shaped structure, the membranous labyrinth (Fig. 384). This contains the sensory apparatus concerned with hearing and also that associated with the sense of equilibrium. The membranous labyrinth lies within the bony labyrinth, a similarly shaped space hollowed out of the petrosal bone (part of the temporal). The membranous labyrinth is filled with a fluid, the endolymph, and is surrounded by a similar fluid, perilymph, which fills the bony labyrinth. The perilymph is separated from the cavity of the middle ear at the fenestrae cochleae and vestibuli, only by the thin membranes covering these windows.

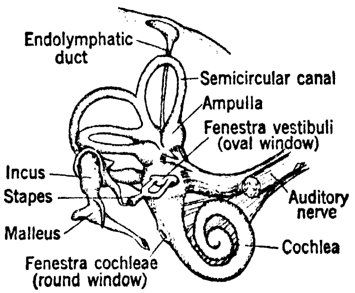


Fig. 384. Diagram of the inner ear of man, showing the relation of the ear bones. (Adapted from the American-Frohse Anatomical Charts, courtesy of A. J. Nystrom and Company, Chicago.)

The labyrinths consist of an expanded central portion, the utriculus (Fig. 385), with which the semicircular canals are

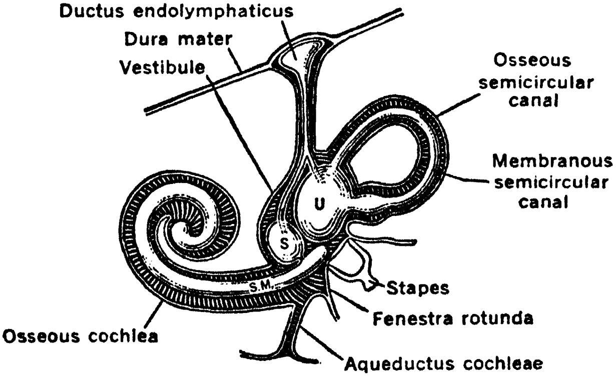


Fig. 385. Diagram of the membranous labyrinth of the inner ear enclosed in the bony labyrinth. S, saccule; U, utriculus; S.M., scala media. (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, by permission of The Macmillan Company, publishers.)

continuous, and a smaller body, the sacculus. From the sacculus a narrow body, the lagena, develops. In mammals, this is drawn out into a tubular, spirally wound cochlea. In man there are about two and one-half turns to the spiral. The semicircular canals are concerned primarily with equilibrium and will be described below. The cochlea contains the sensory cells associated with hearing.

As seen in a cross section of the cochlea (Fig. 386), the cavity of the bony labyrinth is divided into two large spaces containing perilymph and separated from one another by a thick basilar membrane. The space above the basilar membrane is known as the scala vestibuli; that below it, as the scala tympani. These two spaces are connected at the extreme tip of the cochlea by an opening, the helicotrema; consequently, the perilymph of the two spaces is continuous. At the other end (or base) of the cochlea, the perilymph of the scala vestibuli and of the scala tympani is separated from the middle ear by the membranes of the fenestra vestibuli and fenestra cochleae respectively. The membranous labyrinth is above the basilar membrane. The triangular

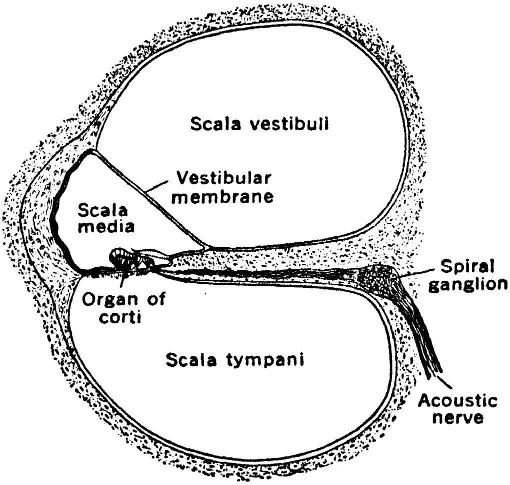


Fig. 386. Diagram of a section of a portion of the cochlea. Note the tectorial membrane extending out over the organ of Corti. (From Kimber, Gray, and Stackpole, *Textbook of Anatomy and Physiology*, by permission of The Macmillan Company, publishers.)

cavity within this is the scala media. The endolymph within the scala media is separated from the perilymph of the scala vestibuli by Reissner's (vestibular) membrane. The outer surface of the scala media is in direct contact with the inner wall of the bony labyrinth and is, therefore, surrounded by perilymph on two sides only.

The organ of Corti (Fig. 387), which contains a series of hair cells together with other protective tissues, is located in the scala media on the basilar membrane. These hair cells constitute the receiving apparatus for this sense. They are supplied by branches of the eighth, or auditory nerve, which reach them by way of the basilar membrane. Extending out into the endolymph above the hair cells is the membrana tectoria, one edge of which is attached at the angle between Reissner's membrane and the basilar membrane, while the other margin is free.

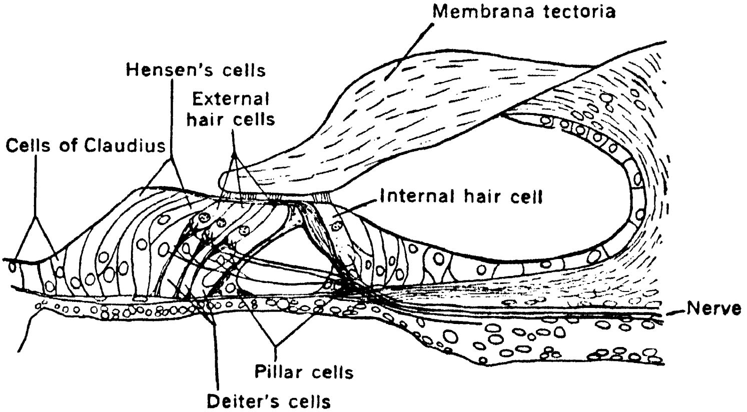


Fig. 387. Cross section through the organ of Corti, within the membranous labyrinth (scala media). (From Walter, *Biology of the Vertebrates*, after Szymonowicz, by permission of The Macmillan Company, publishers.)

These somewhat complicated structures of the ear may be summarized by a brief description of how they probably function in hearing. Sound waves are directed by the pinna into the auditory canal and thus reach the tympanic membrane, causing it to vibrate. These vibrations are carried across the middle ear by means of the auditory ossicles and communicated by the stapes to the membrane over the fenestra vestibuli. Its resulting vibrations set up a wave of vibrations of the perilymph in the scala vestibuli. These may continue through its entire extent, pass by way of the helicotrema to the scala tympani, and eventually be absorbed by the vibration of the membrane covering the fenestra cochleae. These waves in the perilymph affect the thin Reissner's membrane and are transmitted by it to the endolymph of the scala media. Waves in the endolymph in turn initiate an undulating movement of the membrana tectoria, causing it to come in contact with the hairs of the sensory cells in the organ of Corti. The stimulus is then communicated to the sensory neurons and carried as a nerve impulse to that area of the brain concerned with the interpretation of sound.

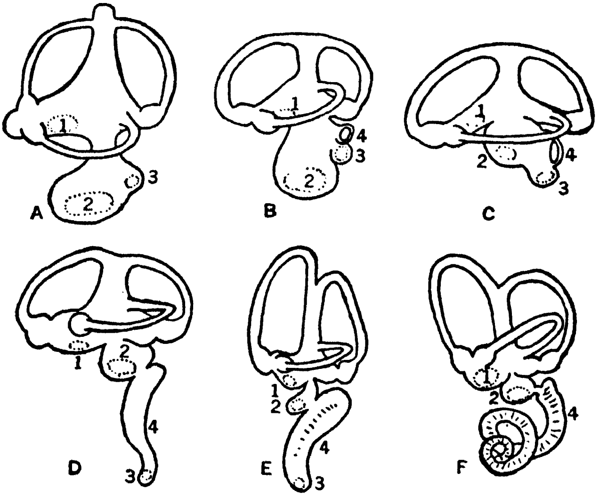


Fig. 388. Diagrams of the left labyrinth of the ear of A, a teleost; B, a frog; C, a turtle; D, a crocodile; E, a bird; F, a mammal. 1, macula utriculi; 2, macula sacculi; 3, macula lagenae; 4, basal papilla. (From Walter, *Biology of the Vertebrates*, after Hesse, by permission of The Macmillan Company, publishers.)

Comparative Anatomy of the Auditory Organ

The ear of cyclostomes and fishes, as aforementioned, is entirely an internal structure, comparable in many respects to the inner ear only and concerned, for the most part, with the sense of equilibrium (Fig. 388).

In the higher amphibians (frogs and toads) for the first time external evidence of an ear appears, in the form of a tympanic membrane which is placed level with the skin. Beneath the membrane is a tympanic cavity comparable to the middle ear of higher vertebrates. Extending across this cavity from the tympanic membrane to that of the fenestra vestibuli is a single bone, the columella, and a cartilage. The inner ear is similar to that of the higher vertebrates except that the lagena, although larger than in the fishes, is still small.

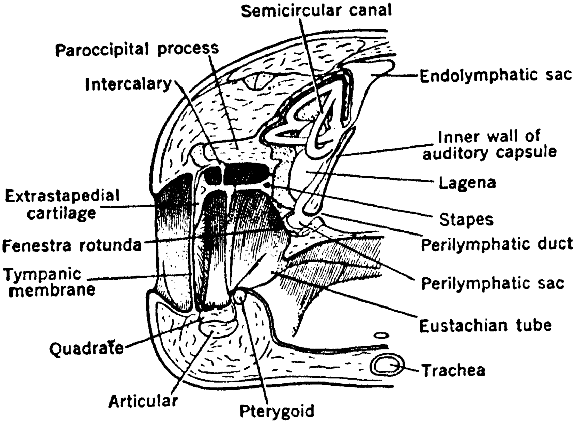


Fig. 389. Transverse section of the head of a lizard, through the tympanic cavity. (From Goodrich, *Studies on the Structure and Development of the Vertebrates*, after J. Versluys, by permission of The Macmillan Company, publishers.)

In the class Reptilia among the lizards (Fig. 389) we find for the first time an external auditory opening. This opens into a short auditory canal at the bottom of which is located the tympanic membrane. Two ear bones are present, either joined or fused together, the outer extracolumella in contact with the tympanic membrane and the inner columella (or plectrum) which fits into the fenestra vestibuli. In the inner ear the lagena has become somewhat lengthened and curved. A rudimentary organ of Corti is present in the alligator.

The ear of the bird is little different from that of reptiles. The auditory canal is more extensive, and the lagena is somewhat longer and slightly curved. The Eustachian tubes join, forming a single duct which opens into the pharynx, as in the alligator.

The mammalian ear has been described in detail. One notable advance is the presence of the three bones in the middle ear; another is the spiral winding of the lagena which forms the cochlea. The single columella of lower forms or the columella and extracolumella of reptiles and birds transfer the vibrations directly and unmodified across the middle ear. The three jointed ossicles of mammals make possible modification of the vibrations in terms of thrust and amplitude.

The Ear as an Organ of Equilibrium

It was stated above that the semicircular canals are concerned with the static sense. They are similar in number and structure in all vertebrates above the cyclostomes. The hagfishes have a single canal, the lampreys two, and all other vertebrates three on each side. Typically, there are two, lying in a vertical plane at right angles to each other, and a third which lies in a horizontal plane. Their cavities containing endolymph are continuous with one another and also with the cavity of the sacculus. A bulblike expanded portion at one end of each canal near the sacculus is known as an ampulla. Within each ampulla lies a projecting structure, composed largely of connective tissue, surmounted by a group of sensory cells. This whole structure is known as the crista. Each crista is supplied by branches of the eighth or auditory nerve. The sensory cells are provided with fine cilia which project into the fluid-filled cavity. Movements of this endolymph affect these hairs which in turn stimulate the sensory cells. Any change in position of the head brings about corresponding movements of the endolymph, which sets up a nerve activity destined to bring about the responses necessary for maintaining or restoring equilibrium.

In some vertebrates the "hairs" are made more sensitive by the presence of otoconia. These are small crystals, or concretions, of calcium which become attached to the "hairs." In many fishes large concretions of this character, known as otoliths or ear stones, are present.

THE ORGAN OF SIGHT

The vertebrate eye is an image-forming or camera type of eye. It is the organ that, with the cooperation of the nervous system, enables us to distinguish objects. A mental image, or picture, of different objects is formed by means of light rays reflected from them to the eye.

Of the various sense organs none shows so little variation throughout vertebrate history as does the eye. Reaching a high degree of development both structurally and functionally in the lower groups of fishes, this structure has been very little modified in the higher classes. The human eye is very similar to that of the fishes as far as the essential parts are concerned. The eyeball is made up of the same three layers, or coats, and it is moved by the same six muscles which are innervated by the same cranial nerves. The most important difference noted is in the shape of the lens. In the fishes the lens is more spherical than it is in terrestrial animals. The spherical lens seems to serve efficiently for a relatively short range of vision in a liquid medium. In the terrestrial vertebrates the lens is more flattened, and the outer and inner surfaces are unequally convex.

Differences in the acuteness of vision in various vertebrates may be due to such factors as the degree of transparency of the skin covering the eye and the differences of location of the orbit rather than to variations in structure of the eye itself.

Because of this similarity of structure in the eyes of the typical representatives of the different vertebrate classes, it will be necessary to describe the eye of one form only. The general anatomical features of the human eye will be considered.

Morphology of the Human Eye

The eye is a spherical body located in an orbit of the skull. It is held in place and subjected to limited movement by the eye muscles previously mentioned. It is covered by the conjunctiva, a thin, transparent area of the skin. As seen in a section (Fig. 390), the eyeball is made up of three layers, or coats. These are, beginning with the most external, the sclera, the choroid, and the retina. The sclerotic coat is a tough protective layer of connective tissue which surrounds a greater part of the eyeball. The anterior portion of this layer is the transparent cornea.

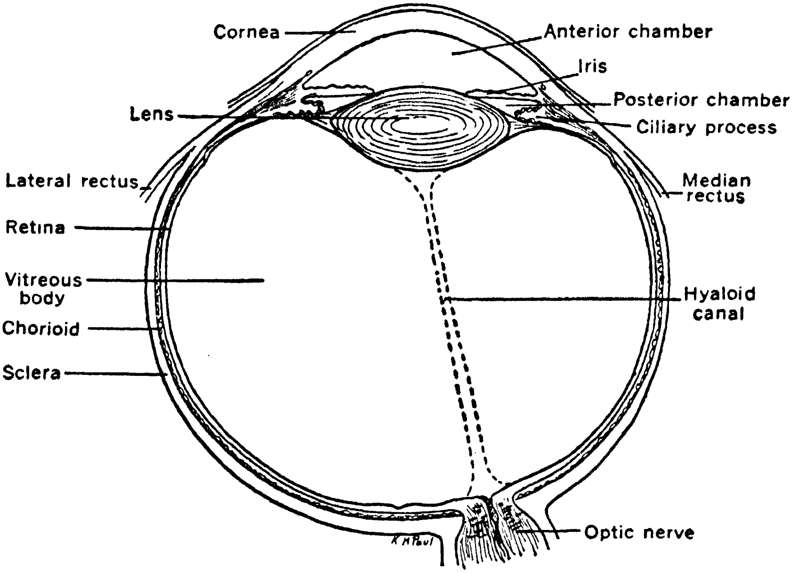


Fig. 390. Horizontal section of the human eye. (Reprinted by permission from *Introduction to Vertebrate Embryology*, Fourth Edition, by W. Shumway, after Howden, published by John Wiley and Sons, Inc.)

The choroid is a highly vascular layer lying just within the sclera. Externally it ends in the ciliary body, which is a circular ridge extending into the cavity of the eyeball at the inner margin of the cornea. The lens is attached to the ciliary body by means of ligaments. The shape of the lens may be changed by the action of these ligaments initiated by the ciliary muscles. These changes of shape are adjustments for near or far vision. The iris is a muscular ring containing near its center a small, circular opening, the pupil. This lies just outside the ciliary body, to which its periphery is attached. The iris acts as a diaphragm, containing as it does both circular and radial muscles. Contraction of the circular muscles decreases the diameter of the pupil. Conversely, the diameter of the pupil is increased by contraction of the radial muscles. In this way the size of the opening through which the rays of light pass to the lens may be regulated.

The innermost layer of the eyeball, the retina, consists largely of the sensory cells which are connected with the endings of the optic nerve. Externally a nonsensory portion of the retina continues as a lining of the ciliary body and iris. The optic nerve leaves the eyeball somewhat medial to its inner pole. As the sensory cells or receptors are not present in this region, it is known as the "blind spot." The area of keenest vision is the macula lutea, located at the true internal pole.

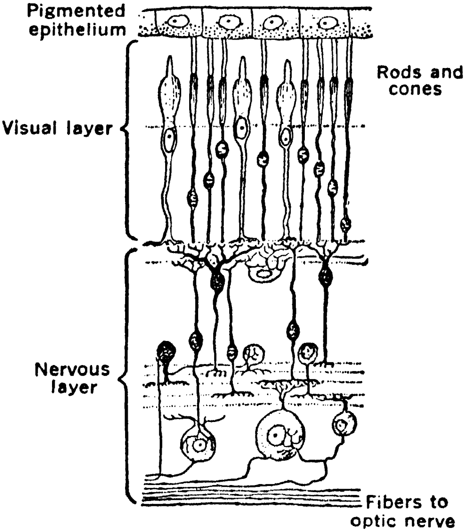


Fig. 391. Diagram of a vertical section of the human retina. (From Woodruff, *Animal Biology*, by permission of The Macmillan Company, publishers.)

Microscopically, the retina (Fig. 391) is a complicated coat containing several layers of different kinds of cells embryologically derived from evagination of the forebrain. Among these may be mentioned the innermost layer of pigmented epithelium, the layer of rod and cone cells, a layer of bipolar nerve cells, and an outer layer of ganglionic cells. The rods and cones are the sensory receiving cells of the eye. Their terminal processes are in contact with the dendrites of the bipolar cells. The axons of the latter are in turn in contact with the processes of the ganglionic cells, the fibers of which form the optic nerve.

internally the eyeball is divided by the lens into two cavities. The outer of these, known as the anterior chamber, is filled with a thin, watery lymph, the aqueous humor. This cavity is partially subdivided by the iris into an anterior and a posterior space. The much larger posterior chamber contains a transparent jellylike material, the vitreous humor (or body). Penetrating the vitreous body from the lens to the point where the optic nerve leaves the eyeball is the hyaloid canal, which represents the position of an artery in embryonic life.

The physiology of sight has not yet been satisfactorily explained, although it is generally considered to be due to chemical changes taking place in a phototropic substance, the visual purple, located in the rods and cones. Light rays entering the eyeball through the transparent cornea and the pupil are refracted on passing through the lens and focussed upon different parts of the retina according to long-established physical laws.

SUMMARY

The sense organs consist primarily of cells which are especially sensitive to environmental changes. The resulting stimulus is passed on to the responding organ by the nervous system. Associated with the sensory cells are various other structures, some of which are protective while others are concerned with increasing or otherwise modifying the stimulus.

The functional unit of a sense organ is a specialized epithelial cell which is associated with the ending of a sensory neuron. Many of these simpler sense organs are located in the dermis where they are associated with the perception of such qualities as heat, cold, touch, pressure, etc. A variety of tactile corpuscles are found in the mammalian skin.

In aquatic vertebrates are found several kinds of sense organs, which are influenced by changes in pressure, and currents in a liquid medium. The lateral line organs of fishes are of this type.

Taste buds are concerned with the perception of such qualities as sweet, bitter, sour, salty, etc. They are usually confined to the surface of the tongue. The organ of smell distinguishes the kinds of odors given off from different bodies. These cells are located in the olfactory membrane which lines the nasal cavity.

The vertebrate ear is concerned with two functions — hearing and equilibrium. The ear of cyclostomes and fishes is an internal structure consisting mainly of the semicircular canals which are associated with the maintenance of equilibrium. In the amphibians a tympanic membrane is present just beneath the skin, and the ear is concerned with the reception of sound waves. In the lizards an external opening is present for the first time, and the membrane is located at the bottom of a tubular cavity. In the mammals the ear consists of three parts, the external, middle, and inner ear. The external ear is distinguished by the presence of a pinna. The middle ear contains three auditory bones, which transmit the sound waves from the membrane to a lymph-filled cavity of the inner ear. The receptor cells are located in the organ of Corti within the inner ear. These cells are stimulated by vibrations passing through the lymph which surrounds them and the resulting nerve excitation is transferred to branches of the auditory nerve and thence to the brain.

The vertebrate eye is an image-forming or camera eye. There is very little variation in the organ of sight from the lowest to the highest vertebrate. It is a more or less spherical body, the wall of which is made up of three layers or coats — the sclera, the choroid, and the retina. The outer layer (sclera) is more or less protective, the middle layer is vascular, and the inner layer contains the sensory cells which are continuous with the optic nerve. The eyeball is hollow, containing two chambers separated by a lens. Rays of light pass through a transparent membrane, the cornea, through an opening, the pupil, to the outer surface of the lens. Passing through the lens, they cross the posterior chamber of the eye to the cells of the retina. The size of the pupil is regulated by a diaphragm, the iris, and the convexity of the surfaces of the lens is also subject to modification. The lens of the fish eye is more nearly spherical than is that of terrestrial vertebrates.

XVI. The Ductless Glands

In the discussion of the nervous system it was stated that the vertebrates are provided with a second mechanism for the regulation and coordination of their various life processes. This type of coordination, which is chemical in nature, is accomplished by the secretions produced by a series of ductless, or endocrine, glands. These so-called internal secretions are elaborated from materials brought to the glands by the

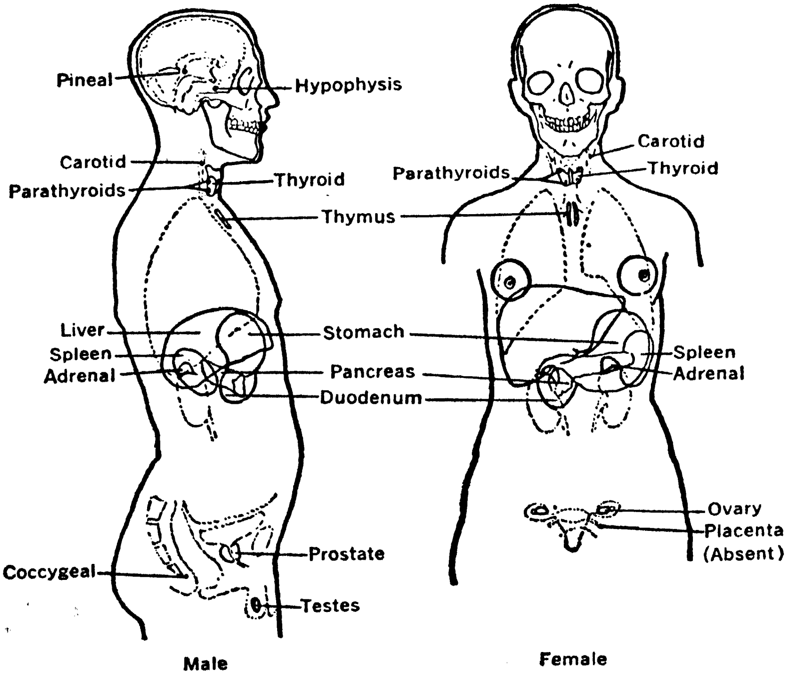


Fig. 392. Diagrams showing the location of the ductless glands. (From Walter, *Genetics*, after chart in *Endocrinology and Metabolism*, edited by L. F. Barker, D. Appleton and Co., by permission of The Macmillan Company, publishers.)

blood and are distributed by the blood throughout the body. Their active constituents, which are known as hormones, may serve either as incitors or inhibitors in influencing the development of the body and also the metabolic processes which characterize the normal life of an animal. The hormones apparently are catalytic in their action; that is, they serve to hasten chemical changes without themselves being modified. Extracts of many of the glands are now successfully used in the treatment of conditions due to a deficiency of their normal secretions. Some of the hormones have also been prepared synthetically and used with satisfactory results.

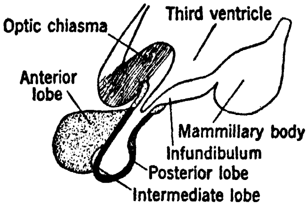


Fig. 393. Diagram showing the relationships of the hypophysis to the adult brain. (Redrawn from Walter, *Biology of the Vertebrates*, after Tilney, by permission of The Macmillan Company, publishers.)

The study of the effects of the secretions of the ductless glands is still in its infancy when compared with what is known of animal physiology in general. In the light of present knowledge of these glands it may be said that they work together in determining the development of the body as a whole and of its secondary sex characteristics, and also that they not only control many of the activities of the different organs, but also influence the behavior of the animal.

According to their location in the body (Fig. 392), the more important ductless glands may be divided as follows:

The head — The pituitary and pineal bodies
The neck — The thyroid and parathyroids
The thorax — The thymus
The abdomen — The suprarenals and the endocrine portions of the pancreas, duodenum, and gonads

GLANDS OF THE HEAD

PITUITARY OR HYPOPHYSIS. The pituitary gland, or hypophysis, is present in vertebrates generally (Fig. 393). It is a compound gland in structure and origin as well as in function. It consists of three parts, the anterior, intermediate, and posterior lobes. Attached to the ventral surface of the brain by the infundibulum, a narrow tubular portion of the diencephalon, it lies in the sella turcica, a depression in the surface of the sphenoid bone. The anterior lobe is of ectodermal origin, developing as an evagination of the roof of the oral cavity. The posterior and intermediate lobes are derived from the brain and remain attached to the infundibulum. There is difference of opinion as to the secretory character of the intermediate lobe. Some associate it functionally with the posterior lobe, while others state that it produces no definite hormone.

The anterior lobe apparently produces two hormones which have different functions. One hormone seems to be concerned with the regulation of growth of the body in general; the other, with the development and functioning of the sex organs. In the young, overproduction of the growth hormone causes giantism as a result, largely, of the lengthening of the bones, while underproduction results in the opposite condition, or dwarfism. In the adult, oversecretion of this hormone causes a condition known as acromegaly, indicated by the abnormal growth, in width, of certain parts of the skeleton, particularly the hands and feet.

The other hormone has been referred to as gonadotropic because of its influence upon the development of the sex cell and the various events which occur during the estrous cycle. There seems to be a rhythmic relationship between the effects produced by this hormone and those attributed to the hormones produced by the Graafian follicle and the corpus luteum. This gonadotropic hormone of the anterior pituitary, which has been named prolan, seems to contain two active principles which may be referred to as prolan-A and prolan-B. The action of these will be briefly discussed in connection with the description of the hormones produced in the female gonad.

The posterior lobe produces a secretion containing pituitrin, which causes a contraction of smooth muscles, particularly those of the blood vessels and of the wall of the uterus. It has frequent use in obstetrics in producing contractions during parturition.

THE PINEAL BODY. This is a small body formed by evagination from the roof of the diencephalon in many vertebrates. Consisting of highly vascular as well as nerve tissue, it has long been suspected of having endocrine functions. Although many different functions have been assigned to it in the past, its exact role remains very much a mystery at the present time. This body in mammals seems to be closely related to, if not the exact homologue of, the parietal organ, or third eye, characteristic of many fossil vertebrates and of the living reptile *Sphenodon*.

GLANDS OF THE NECK

THE THYROID. The thyroid is one of the largest of the ductless glands and is, perhaps, the one best understood at the present time. In mammals generally it consists of two rounded or elliptical lobes which are connected to each other by a narrow band, the isthmus. The lateral lobes lie on either side of the trachea, just posterior to the larynx, the isthmus crossing the trachea ventrally.

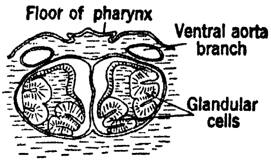


Fig. 394. Cross section through endostyle of an *Ammocoete* larva. (Redrawn from De Beer, *Vertebrate Zoölogy*, by permission of The Macmillan Company, publishers.)

The larval *Petromyzon* (Fig. 394) has a subpharyngeal gland, a part of which develops into a coiled thyroid gland. In fishes the thyroid consists of scattered patches of tissue in the region of the ventral aorta. In higher vertebrates it becomes increasingly more compact and eventually is a bilobed organ, as in the mammals. It arises as an evagination from the pharynx, to which it remains connected, for a time, by a duct. This connection is later lost.

The thyroid affects the rate of metabolism of the body by regulating the rate of oxidation. The hormone thyroxin is rich in iodine. Thyroxin has been extracted and also artificially manufactured and is widely used to alleviate conditions resulting from deficiency of the normal secretion.

Oversecretion, or hyperthyroidism, greatly increases the rate of metabolism, and leads to a condition known as exophthalmic goiter. This is characterized by loss of weight, a rapid pulse, protruding eyeballs, and an extremely nervous condition. Common goiter is an enlargement of the gland itself. Undersecretion, or hypothyroidism, leads to cretinism in children and to myxoedema in adults. In the former condition, both physical and mental growth are retarded, while myxoedema is marked by an increase in weight, loss of hair, muscular weakness, and other evidences of lowered metabolism.

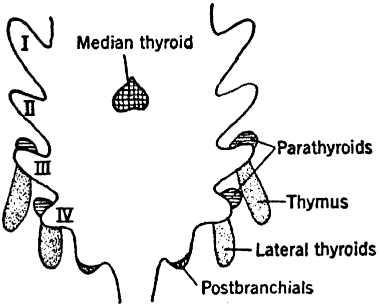


Fig. 395. Diagram showing the origin of various ductless glands from pharyngeal pouches. I–IV, Branchial pouches. (Redrawn from Walter, *Biology of the Vertebrates*, after Kohn, by permission of The Macmillan Company, publishers.)

THE PARATHYROIDS. In man the parathyroids are small, round bodies, usually four in number, on the dorsal surface of the lobes of the thyroid. Embryologically they arise as buds from the pharyngeal pouches (Fig. 395), largely from the third and fourth. Present in all vertebrates above the teleost fishes, they are considered to be homologous to the more numerous but similar epithelial bodies of the lower fishes and the cyclostomes.

The secretion of the parathyroids regulates the calcium metabolism of the body. The complete removal of these glands results in convulsions, tetany, and eventually death.

GLANDS OF THE THORAX

THE THYMUS. The thymus gland is characteristic of all vertebrates and is derived from the dorsal portions of the pharyngeal pouches, particularly from the third (man). In the adult mammal (Fig. 396), the gland is located in the anterior part of the thoracic cavity between the arch of the aorta and the anterior end of the sternum.

The thymus is a relatively large gland in early life. It decreases in size at the time of puberty and eventually may almost entirely disappear. Its exact function is not yet definitely known. Because of the fact that it becomes less important after maturity it has been naturally associated with growth of the body as a whole and more particularly with the development of the sex organs. Its histological character and its plentiful blood supply strongly suggest a lymphatic function.

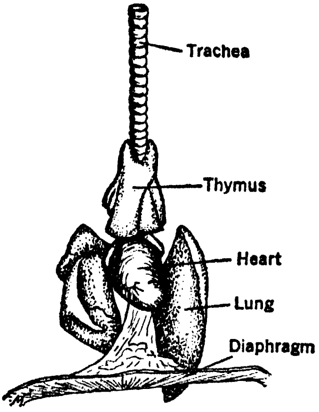


Fig. 396. The thymus gland of the white rat, showing its relation to the heart and lungs.

GLANDS OF THE ABDOMEN

THE SUPRARENALS (ADRENALS). Among the various glands located in the abdomen, the only ones purely endocrine in character are the suprarenals. In mammals these are in the form of small capsules which fit over the anterior ends of the kidneys. They are compound organs consisting of an outer cortex and an inner medulla. These regions have somewhat different origins as well as functions.

The origin of the two regions of these glands is clearly seen in the fishes (Fig. 397), where they appear as two series of glandular bodies closely related to the kidneys. One series, known as chromaffine bodies, is derived from the migrating nerve cells which also give rise to the sympathetic ganglia of this region of the body. Similar bodies apparently form the medullary portion of the suprarenals of higher vertebrates. The other series of bodies known as interrenals are located between the kidneys of fishes. These apparently become the cortex of the suprarenals of the mammals. In amphibians, reptiles, and birds these two kinds of bodies become more and more closely associated with one another until the relation previously mentioned in the mammals is attained.

The function of the medullary portion of the suprarenal has been known for some time. Its hormone, adrenalin, was the first to be isolated and extensively used in medical practice. Injections of adrenalin cause a rise in blood pressure and an acceleration of the heart, and bring about a decided increase in the amount of sugar available for use as an emergency fuel.

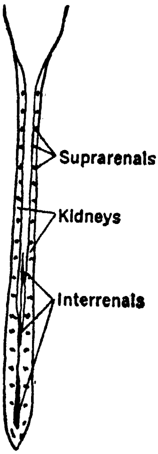


Fig. 397. The kidneys of an elasmobranch, showing suprarenals and interrenals. (From Walter, *Biology of the Vertebrates*, after Grynfeldt, by permission of The Macmillan Company, publishers.)

Although the cortical region of the suprarenals is necessary for life, its exact role has not been definitely established. Quite recently, however, a hormone, cortin, has been extracted from the cortex in a fairly pure state. This has been used with promising results in the treatment of Addison's disease, a formerly fatal malady characterized by muscular weakness, convulsions, and low blood pressure.

THE PANCREAS. This organ has been described previously as one of the largest of the digestive glands. At that time it was stated that portions of the gland, the Islands of Langerhans, are parts of the system of ductless glands. These islands are areas of secretory cells scattered among those which produce the pancreatic juice, which is concerned with digestion. The hormone of the Islands of Langerhans regulates the use of sugar in the body, thereby effecting carbohydrate metabolism. The active principle of the hormone, insulin, has been isolated by Banting and McLeod and is now successfully used in the treatment of diabetes, a disease caused by subnormal activity of the gland.

THE DUODENUM. In addition to its function as a part of the digestive tract, some of the endodermal cells of the duodenum produce a hormone known as secretin. This hormone is distributed by the blood to the liver and pancreas, where it stimulates the production of bile and pancreatic juice respectively.

THE GONADS. In addition to their function in connection with the development of the germ cells, the gonads of both sexes produce internal secretions. While such secretions may not be produced in all vertebrates, in man and other higher forms that have been studied, they are apparently associated with the development of the secondary characteristics which distinguish the sexes, and, in the female, with the changes that follow ovulation and fertilization.

Testes. The site of endocrine formation in the male is in the interstitial cells (Fig. 347), which are located in the spaces between the seminiferous tubules. The hormone produced here is known as testosterone. Removal of the testes in early life prevents the development of many primary and secondary characteristics which distinguish the male from the female.

Ovaries. Two especially important hormones are produced in the ovary: one, known as theelin, is produced in the Graafian follicle; the other, progestin, is formed in the corpus luteum. It is these hormones which were referred to above as playing a conspicuous part in the various changes which occur during the estrous cycle, and following the fertilization of the ovum. Briefly, the series of events is as follows: The production of prolan-A causes the maturing of the Graafian follicle and the subsequent liberation of the mature ovum. This releases theelin from the fluid of the follicle. When theelin reaches its highest concentration in the blood, it inhibits further production of prolan-A in the pituitary. The production of prolan-B now begins and this stimulates the formation of progestin by the corpus luteum. Further production of prolan-B is stopped when the amount of progestin in the blood reaches a certain concentration. At the end of the estrous cycle there is a reduction in the production of both theelin and progestin, so that the formation of prolan-A is no longer inhibited. The cycle is now resumed as prolan-A again stimulates the production of the follicular hormone, theelin. Theelin also apparently plays a part in the early growth of the mammary glands. Progestin, on the other hand, prepares the uterus for the implantation of the ovum (if fertilized) and completes the development of the mammary glands.

SUMMARY

The ductless or endocrine glands play an important part in regulating the various processes of life by chemical means. Their secretions are built up from materials brought to them by the blood stream, and are distributed by the blood stream throughout the body. The action of these hormones is of a catalytic nature. Extracts of the glands and synthetically prepared hormones have been used with satisfactory results, in the treatment of conditions due to a deficiency of the secretion.

The pituitary gland is attached to the ventral surface of the brain. It consists of three lobes, the anterior, the intermediate, and the posterior. The anterior lobe produces several hormones, some of which are concerned with the development of the body as a whole, and others, with the development of the sex organs, and the events of the estrous cycle. The hormone of the posterior lobe, pituitrin, causes contraction of the smooth muscles of the viscera. The function and character of the intermediate lobe is not yet well understood.

The pineal body is attached to the roof of the diencephalon. Although glandular in appearance, its exact function has not been determined. It is perhaps homologous to the third eye of many fossil vertebrates.

In mammals the thyroid gland consists of two lobes which lie on either side of the trachea, posterior to the larynx. They are connected by an isthmus which crosses the trachea ventrally. The thyroid hormone, thyroxin, affects the rate of metabolism by influencing the rate of oxidation.

The parathyroids are small bodies located on the dorsal surface of the thyroids. Their secretion regulates the calcium metabolism of the body.

The thymus gland is located in the ventral part of the thorax just anterior to the heart. This gland is not well understood at the present time, but it seems to be associated with early growth and development of the body.

The suprarenals are located just anterior to the kidneys in the higher vertebrates. They consist of two regions, a cortex and a medulla, which have different origins and different functions. The exact role of the cortical region is not yet definitely known. The hormone of the medullary portion, adrenalin, produces an increase in the amount of sugar available as an emergency fuel.

The Islands of Langerhans are areas of secretory cells located in the pancreas among the other cells which are concerned with the production of pancreatic juice. Their hormone, insulin, regulates the use of sugar in the body and has been successfully used in the treatment of diabetes.

Certain cells of the duodenum produce a hormone, secretin, which influences the secretory activities of the liver and pancreas.

In both sexes portions of the gonads produce internal secretions. The interstitial cells of the testis produce a hormone (testosterone) which is apparently associated with the development of secondary sex characters of the male. Several hormones (theelin, progestin) are produced in the ovary. These have an effect upon the changes which follow ovulation and fertilization.

XVII. The Origin and Evolution of the Vertebrates

A study of the comparative morphology of the vertebrates as presented in the preceding chapters can hardly fail to suggest to the reader the probable course of evolution from fish to man. If the cyclostomes are temporarily left out of the picture, the comparative study of structures indicates a clearly marked line of development from the lowest fishes, through the amphibians, to the reptiles. Here the road forks, one branch leading on to the birds, the other to the mammals. Similarly, within the classes, a comparison of structure is equally convincing in indicating the probable relation among the various orders.

As far as the main trend of vertebrate evolution from the lowest fish to the highest mammal is concerned, there is quite general agreement. Differences of opinion naturally arise, however, concerning the relation of the cyclostomes to the other vertebrates, and also concerning the more general problem of the ancestry of the first vertebrate.

In regard to the question presented by the cyclostomes it has already been seen that they do not seem to fit into the picture of the main line of vertebrate evolution. In tracing the phylogeny of many of the systems of the vertebrate body, it is impossible to go back as far as the cyclostomes. They seem to be the sole survivors of a separate line of development leading into a blind alley which turned out to be a dead-end street. The question naturally arises as to whether the cyclostomes are truly primitive or highly specialized and degenerate animals. The latter interpretation has long been held, but some recent studies on the Ostracoderms, a group of fossil fishes containing the oldest known vertebrates, have caused many to entertain reasonable doubts on this point. These studies have demonstrated many points of similarity between the cyclostomes and the Ostracoderms and indicate at least a close relationship. The possession of heavy armor, a characteristic of these fossil fishes, has long been considered an evidence of racial old age rather than a primitive feature. To hold, as some now do, that the Ostracoderms are directly ancestral to higher vertebrates requires the opposite interpretation, namely, that the exoskeleton is a primitive feature and that the group is a generalized rather than a specialized one. More evidence than has yet been assembled would seem desirable before accepting an idea so radically opposed to long-established beliefs.

The question of the origin of the vertebrates (or chordates) is very old and one that seems to defy a definite and satisfactory answer. It was formerly held that each phylum was derived directly from the preceding phylum. If such is the case, it would follow that the ancestry of the phylum Chordata should be sought in the most highly developed of the preceding phyla, namely, the Arthropoda. Many factors are involved which have combined to make the idea no longer tenable in the opinion of most authorities. The different phyla as arranged by taxonomists at the present time are definite and distinct groups with few if any known species that could be considered to be transitional forms. The typical representatives of the various phyla in existence today are not regarded as sufficiently generalized to have given rise to a type representing a higher phylum. Forms living today may be considered to be the end results of evolution over a long period of time. Furthermore, the paleontologist has not yet succeeded in throwing light on the subject by discovering transitional forms linking one phylum to another. A study of the fossil record, however, has shown that the oldest known vertebrates were in existence as long ago as were many of the representatives of the relatively simple invertebrate phyla. In other words, the geological time table does not indicate an orderly succession of the phyla, as would be expected if one evolved directly from the other.

It seems highly probable, therefore, that the chordate highway branched off from the one leading to the higher nonchordates at an early date in the history of animal life, perhaps as far back as the coelenterates. The many similarities of structure between the two groups may be regarded as due to convergence rather than to immediate ancestry. This belief does not of course preclude descent from a common ancestor, but merely points to a much more distant relationship than would otherwise be the case.

THE ORIGIN OF THE VERTEBRATES

A number of theories of the origin of the vertebrates have been advanced by different scientists. A brief account of the more important of these theories and the evidences upon which they are based follows.

The Annelid Theory

Many writers have attempted to trace the origin of the chordates directly from the annelid worms. In developing this theory, its advocates emphasize the many similarities of structure existing between the chordate embryo and the annelid worm. Both are definitely metameric and bilaterally symmetrical as far as body plan and development are concerned. The nephridia of the lower vertebrates, for example, are very similar to those of the earthworm and have the same relation to the body cavity. The nerve cords are fundamentally alike except for the differences in origin and location. The circulatory systems of the two groups are essentially the same except for the difference in the direction of the flow in the dorsal and ventral vessels.

The proponents of this theory meet these various objections by pointing out that if the annelid worm is inverted, the differences in the relations of structures no longer exist. The annelid nerve cord would then be dorsal to the digestive system, and the blood would flow anteriorly in the ventral blood vessel and posteriorly in the dorsal, as is the case in the chordates. Such a change of position is not without precedent in the animal kingdom, as the squid and the horseshoe crab swim in an inverted position as compared with their typical relatives. Even among the mammals we find that the sloth is apparently much happier and certainly more efficient in locomotion when suspended upside down from the branches of a tree.

On the other hand, this inversion of the annelid makes necessary the development of a new mouth on the new ventral surface to establish the typical vertebrate relationship between the brain and the anterior opening of the digestive tract. It has been pointed out that the vertebrate mouth develops rather late in embryonic life and that the neuropore of the vertebrate embryo and of *Amphioxus* may well represent the annelid mouth.

The absence of a notochord and of definite branchial respiratory devices in the annelids has been deemed by most authorities to be sufficient grounds for rejecting the theory of annelid ancestry for the chordates. A bundle of fibers known as the Faserstrang, which apparently serves as a support to the nerve cord, has been demonstrated in the annelids. This has been compared to the notochord by some, but its development does not bear out the suggested homology.

The Arthropod Theory

The late Dr. Patten of Dartmouth was undoubtedly the leading advocate of this theory. The theory is based upon unquestioned similarities of structure between the Ostracoderms, a group of fossil fishes previously mentioned, and an Arachnid (*Limulus*, the horseshoe crab) together with its extinct relatives the Euripterids. In a series of striking diagrams Patten has illustrated similarities between the two apparently unrelated groups in skeletal structures, appendages, brain, cranial nerves, sense organs, heart, and arteries.

Although the theory of arthropod ancestry of the vertebrates is not generally accepted, the importance of the researches of Patten and more recently of Stensio can hardly be overestimated. Their contributions to our knowledge of the Ostracoderms have suggested the possibility of a new conception of the relations of this group to the cyclostomes and in turn of the relation of the cyclostomes to the other vertebrates.

Other Theories

Among other and less generally accepted theories of vertebrate origin may be mentioned the Nemertean worm theory, advocated by Hubrecht. In this group of worms, which are closely related to the Platyhelminthes, two lateral nerve cords and a single dorsal nerve cord are present. It has been suggested that the anterior end of the dorsal cord enlarged to form the brain of the chordates, and that the lateral cords persisted as the lateral branches of the Vagus nerve. There are few if any points of similarity between the two groups as far as other structures are concerned.

The striking similarity apparent between the larvae of *Balanoglossus* and of the starfish has led some to believe that the echinoderms are ancestral to the vertebrates. These close resemblances strongly point to some relationship between *Balanoglossus* and the echinoderms, but the position of *Balanoglossus* itself in relation to the other chordates is quite uncertain. It is not improbable that a common ancestral form gave rise to the echinoderms on the one hand and to *Balanoglossus* on the other, and that the vertebrates branched off from the road leading to *Balanoglossus*.

The Amphioxus Theory

In many instances in the preceding pages it has been pointed out that *Amphioxus* is fundamentally similar to a typical vertebrate in many of its structures. These resemblances are so obvious as to leave little doubt as to the probable close relation of *Amphioxus* to the vertebrates. This does not mean that *Amphioxus* is directly ancestral to the vertebrates, but rather that the latter have probably developed from an *Amphioxus*-like form.

In an interesting discussion of this possibility, Newman brings out the fact that the existing *Amphioxus* represents dual tendencies in its mode of life. Some of the time they are active, free-swimming animals; at other times they are stationary, remaining in their burrows with the anterior end protruding, waiting for food to be brought to them in the currents of water. Newman suggests that these two opposite lines of development may well have been followed from an ancestral form resembling *Amphioxus*. Certain descendants may have remained near the shore and thus have been subjected to tidal currents, or they may even have migrated to a flowing stream where they were influenced by movements of the water. It is generally agreed that such environmental conditions tend to stimulate the development of active types of animal life. This evolutionary highway, therefore, may have led directly to the primitive fishes, with a side road branching off to the cyclostomes.

On the other hand, other descendants may have been carried into deeper or quieter waters where conditions were more favorable for the development of sedentary or sessile types. This line of evolution may have culminated in such forms as the tunicates. This interpretation would make *Amphioxus*, or at least its parent stock, the direct ancestor of the tunicates, a belief which is not generally held.

Granting that *Amphioxus* is close to the main line of evolution, the question of the origin of the chordates still is unanswered. The *Amphioxus* theory in itself does not disclose the relation between the chordates and the nonchordate phyla. In the light of our present knowledge a combination of several theories may well be as probable as any one of them. In the absence of truly transitional forms to link the phyla definitely together, the known facts suggest that the chordates branched off from the evolutionary highway leading from the coelenterates to the echinoderms. The evidence presented by *Balanoglossus* substantiates its claim as a kind of connecting link in this connection. From *Balanoglossus* on to the tunicates and *Amphioxus*, the evidence is less convincing. If we follow the suggestion of Newman as mentioned above and regard the tunicates as a degenerate offshoot from the *Amphioxus* stock, one difficulty will be obviated. This solution, however, still leaves unexplained the relation between *Balanoglossus* and *Amphioxus*. About all that can be said on this point is that probably both are branches of the main chordate line leading from the coelenterate-echinoderm highway.

With this combination of facts and possibilities before us, probably the only sure statement that can be made at the present time is that the real ancestor of the vertebrates is still unknown. Unless numerous missing links are uncovered by future discovery and investigation, the question of the origin of the chordates may well remain an unsolved problem.

SUMMARY

A study of the comparative anatomy of vertebrates furnishes convincing evidence of the relation of the different classes to one another and of the probable course of evolution from the lower to the higher vertebrates. The cyclostomes do not fit into this picture very satisfactorily, and there is difference of opinion as to whether they are primitive or specialized forms.

The problem of the origin of the vertebrates has not yet been solved. It was formerly believed that each phylum was derived directly from a preceding phylum. This belief is no longer held, as transitional forms are unknown. It is thought that the chordates branched off from the line leading to the higher non-chordates as far back as the coelenterates.

Various theories concerning vertebrate ancestry have been held by scientists at different times. The more important of these are the Annelid and the Arthropod theory. These theories have both had substantial backing, as they are based upon rather striking morphological similarities. It is probable that these similarities can be explained by convergence rather than by direct ancestry. Other minor theories are the Nemertean worm and the Echinoderm theory. The latter emphasizes the similarity of the larval stages of *Balanoglossus* and certain echinoderms. This does not explain the relation of the vertebrates to *Balanoglossus*.

The many resemblances of *Amphioxus* to the vertebrates points to a close relationship between them, but do not solve the problem of the immediate ancestry of the vertebrates.

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